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TABLE OF CONTENTS

Volume 105

Anderson, William D., Jr., Patricia J. Kailola, and Bruce B. Collette. Two new snappers (Teleostei: Lutjanidae: Apsilinae): *Paracaesio paragrapsimodon* Anderson and Kailola from the western Pacific and *P. waltervadi* Anderson and Collette from the western Indian Ocean 443–461

Banks, Richard C. and Carla J. Dove. The generic name for Crested Caracaras (Aves: Falconidae) 420–425

Bannikov, Alexandre F. and James C. Tyler. *Caprovesposus* from the Oligocene of Russia: the pelagic acronurus presettlement stage of a surgeonfish (Teleostei: Acanthuridae) 810–820

Barr, Cheryl B. and Paul J. Spangler. A new genus and species of stygobiontic dryopid beetle, *Stygoparnus comalensis* (Coleoptera: Dryopidae), from Comal Springs, Texas 40–54

Bishop, Gale A. Two new crabs, *Homolopsis williamsi* and *Homolopsis centurialis* (Crustacea: Decapoda), from the Western Interior Cretaceous of the United States 55–66

Bishop, Gale A. A new Cretaceous crab, *Diaulax millerae* (Crustacea: Decapoda), from the Northern Atlantic Coastal Plain, U.S.A. 555–561

Blake, James A. New species and records of Phyllodocidae (Polychaeta) from the continental shelf and slope off California 693–708

Blake, James A. and Nancy J. Maciolek. Polychaeta from deep-sea hydrothermal vents in the eastern Pacific. III. A new genus and two new species of Spionidae from the Guaymas Basin and Juan de Fuca Ridge with comments on a related species from the western North Atlantic 723–732

Bowman, Thomas E. and James J. Orsi. *Deltamysis holmquistae,* a new genus and species of Mysidacea from the Sacramento-San Joaquin estuary of California (Mysidae: Mysinae: Heteromysini) 733–742

Brooks, Daniel R., Joao Batisto Catto, and Jose F. R. Amato. A new phylogenetic classification of the genera of the Proterodiplostomidae Dubois, 1936 (Digenea: Strigeiformes) 143–147

Brown, Walter C., Michael McCoy, and Gordon H. Rodda. A new *Lepidodactylus* (Reptilia: Gekkonidae) from Guadalcanal Island, Solomons 440–442

Browning, M. Ralph. A new subspecies of *Chamaea fasciata* (Wrentit) from Oregon (Aves: Timaliinae) 414–419

Campbell, Jonathan A. and Dwight P. Lawson. *Hyla bocourti* (Mocquard, 1899), a valid species of frog (Anura: Hylidae) from Guatemala 393–399

Campos, Ernesto, Alma Rosa de Campos, and Jorge Ramirez. Remarks on distribution and hosts for symbiotic crustaceans of the Mexican Pacific (Decapoda and Isopoda) 753–759

Campos, Martha R. New species of fresh-water crabs of the genus *Neostrengeria* (Crustacea: Decapoda: Pseudothelphusidae) from Colombia 540–554

Chapman, Joseph A., Kenneth L. Cramer, Nico J. Dippenaar, and Terence J. Robinson. Systematics and biogeography of the New England cottontail (*Sylvilagus transitionalis*) (Bangs, 1895), with the description of a new species from the Appalachian mountains 841–866

Couri, Mácia Souto and Paulo Francisco de Araújo. The immature stages of *Antherigona orientalis* Schiner (Diptera: Muscidae) 490–493

Criales, Maria M. Redescription of the hippolytid shrimp *Trachycaris rugosa* (Bate) (Crustacea: Decapoda: Caridea) from the western Atlantic, with notes on sexual dimorphism 562–570

Dean, Harlan K. A new arabellid polychaete living in the mantle cavity of deep-sea wood boring bivalves (family Pholadidae) 224–232

Donnelly, Maureen A., Roy W. McDiarmid, and Charles W. Myers. A new lizard of the genus *Arthrosaura* (Teiidae) from southern Venezuela 821–833

Donovan, Stephen K. Jamaican Cretaceous Echinoidea (Echinodermata). 3. *Scoliechinus axiologus* Arnold and Clark, 1927, and an indeterminate cassiduloid 23–31

Eibye-Jacobsen, Danny. Phyllodocids (Annelida: Polychaeta) of Belize, with the description of three new species 589–613

Engstrom, Mark D., Oscar Sánchez-Herrera, and Guillermina Urbano-Vidales. Distribution, geographic variation, and systematic relationships within *Nelsonia* (Rodentia: Sigmodontinae) 867–881

Erséus, Christer and Michael R. Milligan. A new species of *Coralliodrilus* (Oligochaeta: Tubificidae) from the eastern Gulf of Mexico, and a new record of *C. corpulentus* from South Carolina 585–588

Fernandez-Leborans, Gregorio and Apolonia Novillo. Morphology and taxonomy of two new species of marine ciliates (Ciliophora: Spirotrichea: Stichotrichida: Amphisiellidae) 165–179

Ferrari, Frank D. and Julie W. Ambler. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Farran, 1913) (Oithonidae) from a mangrove cay in Belize 275–298

Fitzhugh, Kirk. On the systematic position of *Monroika africana* (Monro) (Polychaeta: Sabellidae: Fabriciinae) and a description of a new fabriciin genus and species from Australia 116–131

Fitzpatrick, J. F., Jr. A new crawfish of the genus *Orconectes* from east-central Mississippi and adjacent Alabama (Crustacea: Decapoda: Cambaridae) 780–787

Fitzpatrick, J. F., Jr., and Royal D. Suttkus. A new crawfish of the genus *Orconectes* from the Yazoo River system of Mississippi (Decapoda: Cambaridae) 70–76

Flint, Oliver S., Jr. Studies of Neotropical caddisflies, XLIX: The taxonomy and relationship of the genus *Eosericostoma,* with descriptions of the immature stages (Trichoptera: Helicophidae) 494–511

Flint, Oliver S., Jr. A review of the genus *Chloronia* in Costa Rica, with the description of two new species (Neuropterida: Megaloptera: Corydalidae) 801–809

Frame, Ann B. The lumbrinerids (Annelida: Polychaeta) collected in two northwestern Atlantic surveys with descriptions of a new genus and two new species 185–218

Froeschner, Richard C. The flat bug genus *Calisiopsis* Champion: A review with descriptions of three new species, including one from Dominican Republic amber (Heteroptera: Aradidae) 32–39

García, Eduardo López and Guillermo San Martín Peral. A new species of *Dentatisyllis* (Syllidae: Polychaeta) from Cape Verde Islands, West Africa 219–223

Garth, John S. and Thomas M. Iliffe. *Guitonia troglophila,* a new genus and species of anchialine crab from the Galápagos, Isla Santa Cruz, Grieta de Caleta la Torta (Crustacea: Brachyura) 310–316

Goedert, James L. and Ross E. Berglund. Miocene fossils of the genus *Cancer* (Decapoda: Cancridae) from northwestern Washington, U.S.A. 67–69

Graves, Gary R. Diagnosis of a hybrid antbird (*Phlegopsis nigromaculata* × *Phlgopsis erythroptera*) and the rarity of hybridization among suboscines 834–840

Green, Timothy M. *Pinnaxodes gigas,* a new species of pinnotherid crab from the Gulf of California (Decapoda: Brachyura: Pinnotheridae) 775–779

Hilbig, Brigitte. New polychaetous annelids of the families Nereididae, Hesionidae, and Nephtyidae from the Santa Maria Basin, California, with a redescription of *Glycera nana* Johnson, 1901 709–722

Hobbs, Horton H., Jr. and Richard Franz. *Procambarus (Ortmannicus) attiguus,* a new troglobitic crayfish (Decapoda: Cambaridae) from the Saint Johns River basin, Florida 359–365

Hsieh, Hwey-Lian. *Pseudopolydora diopatra,* a new species (Polychaeta: Spionidae) from Taiwan 630–635

Humes, Arthur G. *Euryte verecunda,* new species (Copepoda: Cyclopoida), associated with the coral *Porites lobata* on the Pacific coast of Panama 268–274

Ishida, Teruo. Cyclopoid and harpacticoid copepods (Crustacea) from southeastern Alaska, U.S.A. 249–254

Iverson, John B. and William P. McCord. A new subspecies of *Cuora galbinifrons* (Testudines: Batagurinae) from Hainan Island, China 426–432

Iverson, John B. and William P. McCord. A new Chinese eyed turtle of the genus *Sacalia* (Batagurinae: Testudines) 433–439

Kelt, Douglas A. and R. Eduardo Palma. A plea for adequate citation of authors of taxa in systematic studies 411–413

Kensley, Brian and Tomoyuki Komai. Redescription of *Calocarides soyoi* (Yokoya, 1933) from Japan (Crustacea: Decapoda: Axiidae) 81–85

Knapp, Leslie W. Status of type specimens of *Platycephalus rodericensis* Cuvier, 1829 and *P. borboniensis* Cuvier, 1829 (Pisces: Platycephalidae) 389–392

Kornicker, Louis S. *Thaumatoconcha pix*, a new bathyal and abyssal species from off SE Australia (Ostracoda: Halocyprida: Thaumatocyprididae) 233–239

Lara, Marcia, Michael A. Bogan, and Rui Cerqueira. Sex and age components of variation in *Proechimys cuvieri* (Rodentia: Echimyidae) from northern Brazil 882–893

Lemaitre, Rafael and Gabriel E. Ramos. A collection of Thalassinidea (Crustacea: Decapoda) from the Pacific coast of Colombia, with description of a new species and a checklist of eastern Pacific species 343–358

López-González, P. J., M. Conradi, S. Naranjo, and J. C. García-Gómez. A new species of *Anthessius* (Copepoda: Poecilostomatoida) associated with *Berthella stellata* (Risso, 1826) (Gastropoda: Opisthobranchia) 240–248

Manning, Raymond B. A new geryonid crab from Walters Shoals, southwestern Indian Ocean (Crustacea: Decapoda: Brachyura) 86–89

Manning, Raymond B. A new genus for *Corallianassa xutha* Manning (Crustacea: Decapoda: Callianassidea) 571–574

Mathis, Wayne M. and László Papp. A new genus of Periscelididae (Diptera) from the Neotropics 366–372

McCord, William P. and John B. Iverson. A new species of *Ocadia* (Testudines: Bataguridae) from Hainan Island, China 13–18

McLaughlin, Patsy A. A reassessment of *Pagurus tricarinatus* (Stimpson, 1858) (Crustacea: Decapoda: Anomura: Paguridae) 795–800

Melo-Filho, Gustavo Augusto S. de and Gustavo Augusto S. de Melo. Designation of lectotypes for the species of *Munida* (Crustacea: Anomura: Galatheidae) collected by the U.S. Coast Survey Steamer *Blake* (1877–1879) and the description of a new species 512–520

Melo-Filho, Gustavo Augusto S. de and Gustavo Augusto S. de Melo. Reexamination of the material of *Munida* Leach (Crustacea: Anomura: Galatheidae) collected by the H. M. S. *Challenger* (1872–1876) along the Brazilian coast 760–774

Morse, M. Patricia and Jon L. Norenburg. Observations on and redescriptions of *Meiomenia arenicola* Salvini-Plawen, 1985 (Mollusca: Aplacophora), in interstitial solenogaster from Fort Pierce, Florida 674–682

Ng, Peter K. L. The freshwater crabs and palaemonid prawns (Crustacea: Decapoda) of Batam Island, Riau Archipelago, Indonesia, including description of two new species 788–794

Ohtsuka, Susumu. *Tortanus (Acutanus) angularis*, new subgenus and new species (Copepoda: Calanoida), from the Caribbean Sea, with remarks on the subgenera in the genus *Tortanus* 255–267

Parapar, Julio and Guillermo San Martín. *Grubeosyllis celiae*, a new species of Exogoninae (Syllidae: Polychaeta) from off Ceuta, Spain 112–115

Pawson, David L. and Yulin Liao. Molpadiid sea cucumbers of China, with descriptions of five new species (Echinodermata: Holothuroidea) 373–388

Pawson, David L. and John E. Miller. *Phyllophorus (Urodemella) arenicola*, a new sublittoral sea cucumber from the southeastern United States (Echinodermata: Holothuroidea) 483–489

Pettibone, Marian M. Two new genera and four new combinations of Sigalionidae (Polychaeta) 614–629

Reid, Janet W. and Brian H. Kay. *Mesocyclops guangxiensis*, new species, and new records of four congeners (Crustacea: Copepoda: Cyclopidae) from China, Laos, and Viet Nam 331–342

Robinson, Harold. Notes on Lynchnophorinae from Minas Gerais, Brazil, A synopsis of *Lychnophoreopsis* Schultz-Bip., and the new genera *Anteremanthus* and *Minasia* (Vernonieae: Asteraceae) 640–652

Robinson, Harold. Two new species of *Chrysolaena* from Brazil (Vernonieae: Asteraceae) 657–663

Roccatagliata, Daniel and Richard W. Heard. *Diastylopsis goekei*, a new species (Crustacea: Cumacea: Diastylidae) from Antarctic waters 743–752

Rodriguez, Gilberto and Angel L. Viloria. *Chaceus cesarensis,* a new species of freshwater crab (Crustacea: Decapoda: Pseudothelphusidae) from Colombia with a key to the genus 77–80

Rodrigues, Sérgio de A. and Raymond B. Manning. Two new callianassid shrimps from Brazil (Crustacea: Decapoda: Thalassinidea) 324–330

Rodrigues, Sérgio de A. and Roberto Munehisa Shimizu. Description of a new *Axianassa* (Crustacea: Decapoda: Thalassinidea) from Brazil, and its first larval stage 317–323

Ross, Charles A. Designation of a lectotype for *Crocodylus raninus* S. Müller and Schlegel (Reptilia: Crocodylidae), the Borneo crocodile 400–402

Ruedas, Luis A. and John W. Bickham. Morphological differentiation between *Rhogeessa minutilla* and *R. tumida* (Mammalia: Chiroptera: Vespertilionidae) 403–409

Rützler, Klaus and Kathleen P. Smith. Guide to western Atlantic species of *Cinachyrella* (Porifera: Tetillidae) 148–164

Sassaman, Clay. Description of the mature female and epicaridium larva of *Cabirops montereyensis* Sassaman from northern California (Crustacea: Isopoda: Cabiropidae) 575–584

Schotte, Marilyn. *Serolis apheles,* a new species (Isopoda: Serolidae) from the southwest Indian Ocean, and a range extension for *Serolis antarctica* Beddard, 1884 90–96

Sterrer, Wolfgang. Clausognathiidae, a new family of Gnathostomulida from Belize 136–142

Sterrer, Wolfgang. *Lurus minos,* the first species of Luridae (Turbellaria: Rhabdocoela) from the Old World 636–639

Stuck, Kenneth C., Harriet M. Perry, Lidia M. Stuck, and Adeline A. Barrett. Larval development of the Golden Crab, *Chaceon fenneri* (Manning & Holthuis, 1984) (Decapoda: Brachyura: Geryonidae), reared in the laboratory 521–539

Tighe, Kenneth A. *Boehlkenchelys longidentata,* a new genus and species of chlopsid eel (Teleostei: Anguilliformes) from the Indo-West Pacific region 19–22

Toda, Tatsuki, Tomoyuki Miura, and Takahisa Nemoto. *Hyphalion sagamiense,* a new species of Clausidiidae (Copepoda: Poecilostomatoida) associated with a vesicomyid bivalve from the Hatsushima cold-seep site in Sagami Bay, Japan 102–111

Tyler, James C., Robert W. Purdy, and Karl H. Oliver. A new species of *Sphoeroides* pufferfish (Teleostei: Tetraodontidae) with extensive hyperostosis from the Pliocene of North Carolina 462–482

Vecchione, Michael, Bruce H. Robison, and Clyde F. E. Roper. A tale of two species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae) 683–692

Vega-Pérez, L. Amelia and Thomas E. Bowman. Descriptions of the pelagic copepod, *Ctenocalanus heronae* Vega-Pérez and Bowman, from off São Paulo, Brazil (Calanoida: Clausocalanidae) 97–101

Wasshausen, Dieter C. Three new species of *Justicia* (Acanthaceae) from Brazil 664–673

Westheide, Wilfried and Günter Purschke. *Microphthalmus simplicichaetosus* (Annelida: Polychaeta), a new hesionid from the northwestern American Pacific coast with exclusively simple chaetae 132–135

Williams, Ernest H., Jr. and Lucy Bunkley-Williams. *Renocila loriae* and *R. richardsonae* (Crustacea: Isopoda: Cymothoidae), external parasites of coral reef fishes from New Guinea and the Philippines 299–309

Woodman, Neal and Robert M. Timm. A new species of small-eared shrew, genus *Cryptotis* (Insectivora: Soricidae), from Honduras 1–12

INDEX TO NEW TAXA

VOLUME 105

(New taxa are indicated in *italics*; new combinations designated n.c.)

PLATYHELMINTHES

Lurus *minos* 636

GNATHOSTOMULIDA

Clausognathia 137
    suicauda 137

ANNELIDA

Polychaeta

Abyssoninoe *winsnesae* 189
Dentatisyllis *junoyi* 219
Eranno *petersenae* 193
Eteone *brigitteae* 694
    leptotes 696
    pigmentata 696
Eumida *muriatica* 598
Grubeosyllis *celiae* 112
Gyptis *plurisetis* 712
Labioleanira 619
    tentaculata n.c. 624
    yhleni n.c. 621
Labiosthenolepis 614
    laevis n.c. 615
    sibogae n.c. 618
Lindaspio 724
    dibranchiata 724
    southwardorum 727
    carunculata n.c. 729
Lugia *uschakovi* 700
Lumbricalus 195
Microphthalmus *simplicichaetosus* 132
Nephtys *signifera* 719
Nereiphylla *mimica* 605
Nereis *ligulata* 709
Parafabricia 118
    ventricingulata 119
Pholadiphila 224
    turnerae 225
Podarkeopsis *perkinsi* 715
Protomystides *mariaensis* 702
Pseudopolydora *dioatra* 630
Scoletoma acicularum n.c. 204
    hebes n.c. 210
Sige *belizensis* 605
    pleijeli 705

Oligochaeta

Coralliodrilus *priscus* 587

ARTHROPODA

Crustaceae

Anthessius *arcuatus* *240*
Axianassa *australis* 317
Biffarius *delicatulus* 324
Chaceon *collettei* 86
Chaceus *cesarensis* 77
Corallichirus 571
    hartmeyeri n.c. 571
    placidus n.c. 571
    xuthus n.c. 571
Deltamysis 733
    holmquistae 734
Diastylopsis *goekei* 743
Diaulax *millerae* 556
Eucalliax *cearaensis* 327
Euryte *verecunda* 268
Guitonia 310
    troglophila 311
Homolopsis *centurialis* 59
    williamsi 57
Hyphalion *sagamiense* 103
Irmengardia *nemestrinus* 791
Mesocyclops *guangxiensis* 331
Neaxius *frankeae* 344
Neostrengeria *aspera* 540
    gilberti 542
    libradensis *appressa* 543
    lobulata 544
    macarenae 546
    tencalanensis 547
    tonensis 550
Orconectes (Gremicambarus) *jonesi* 780
Orconectes (Hespericambarus) *hartfieldi* 70
Parathelphusa *batamensis* 789
Pinnaxodes *gigas* 775
Procambarus (Ortmannicus) *attiguus* 359
Renocila *loriae* 299
    richardsonae 301
Serolis *apheles* 90
Thaumatoconcha *pix* 234
Tortanus (Acutanus) *angularis* 256
Tortanus (*Acutanus*) 264
Tortanus (*Atortus*) 265

Insecta

Calisiopsis *brodzinskyorum* 34
    kormilevi 36
    nigrotuberculata 38
Chloronia *absona* 807
    osae 805
Parascutops 368
    maculipennis n.c. 371
Stygoparnus 41
    comalensis 47

ECHINODERMATA

- Caudina *atacta* 381
  - *zhejiangensis* 381
- Molpadia *changi* 374
  - *guangdongensis* 377
- Paracaudina *delicata* 384
- Phyllophorus (Urodemella) *arenicola* 484

CHORDATA

Pisces

- *Boehlkenchylys* 19
  - *longidentata* 20
- Paracaesio *paragrapsimodon* 446
  - *waltervadi* 446
- Sjphoeroides *hyperostosus* 465

Reptilia

- Arthrosaura *synaptolepis* 822
- Cuora galbinifrons *serrata* 434
- Lepidodactylus *flaviocularis* 440
- Ocadia *philippeni* 13
- Sacalia *pseudocellata* 426

Aves

- Chamaea fasciata *margra* 417

Mammalia

- Cryptotis *hondurensis* 2
- Sylvilagus *obscurus* 858

PLANTAE

- *Anteremanthus* 646
  - hatschbachii n.c. 646
- Chrysolaena *hatschbachii* 658
  - *nicolackii* 660
- Justicia *andersonii* 666
  - *harleyi* 669
  - *matogrossensis* 671
- Lychnophoriopsis candelabrum n.c. 644
  - damazioi n.c. 644
  - *hatschbachii* 644
- *Minasia* 648
  - alpestris n.c. 650
  - *pereirae* 650

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A NEW SPECIES OF SMALL-EARED SHREW, GENUS *CRYPTOTIS* (INSECTIVORA: SORICIDAE), FROM HONDURAS

Neal Woodman and Robert M. Timm

Abstract.—We describe a new species of small-eared shrew, *Cryptotis hondurensis,* from high elevation pine forest on the western slope of Cerro Uyuca, Francisco Morazán Province, southcentral Honduras. The new shrew is most similar in outward appearance to *C. gracilis,* from which it can be distinguished by cranial and dental features, particularly a shorter, broader mandible with a coronoid process that meets the ramus at nearly a right angle and an m3 with a simple talonid. Cranially, the new species is most similar to *C. nigrescens merriami,* but differs from this species in its longer tail and several cranial and dental features, including a more complex M3. The holotype of the new species had been identified as *C. gracilis* and represented the only specimen of that species north of Costa Rica. Its recognition as a distinct species removes *C. gracilis* from the known fauna of Honduras. The other species of *Cryptotis* presently known from Honduras are *C. nigrescens merriami* and *C. parva orophila.*

Resumen.—Se describe una nueva especie de musaraña, *Cryptotis hondurensis* (Insectivora: Soricidae), del bosque montanoso de la ladera occidental del Cerro Uyuca, Francisco Morazán, Honduras. Externamente, la nueva especie es similar a *C. gracilis* pero se diferencia de *C. gracilis* en características craniales y dentales; en particular, en la presencia de una mandíbula mas corta y mas ancha y con un proceso coronoides que se junta con la rama mandibular en un ángulo de casi 90 grados. Además, m3 presenta una talonida simple. El cráneo de la nueva musaraña se semejante al de *C. nigrescens merriami* pero la nueve especie defiere de *C. nigrescens merriami* por su cola mas larga y en varias características craniales y dentales incluyendo M3 con una corona mas compleja. El holotipo de la nueva especie había sido identificado como *C. gracilis* y este especimen era el único representante de esta especie al norte de Costa Rica. El reconocimiento de este especimen como una especie distinta, limita la distribución de *C. gracilis* a Costa Rica y Panamá y la remueve de la fauna de Honduras. Las otras especies de *Cryptotis* que habitan en Honduras son *C. nigrescens merriami* y *C. parva orophila.*

Small-eared or least shrews of the genus *Cryptotis* (Insectivora: Soricidae) are widely distributed in North America, Central America, and northern South America. They are found in extreme southern Ontario, across much of the eastern and midwestern United States, through eastern, central, and southern Mexico, at high elevations in Central America, and in the northern Andean highlands. The systematics of the Neotropical species are problematic, in part because few specimens have been available, and individual and geographic variation has been difficult to evaluate. Choate (1970) recognized eight species of *Cryptotis* from Mexico and Central America. His monograph was the first comprehensive revision of any group in the genus, providing an important framework for study of these shrews.

One of the most poorly known species of Neotropical *Cryptotis, C. gracilis,* was reported by Choate (1970) as ranging from southern Honduras to western Panama. Among the specimens he referred to *C. gracilis* were one specimen from southern Honduras, 38 from Costa Rica, and three from western Panama. The acquisition of additional specimens of *C. gracilis* from Costa Rica and Panama prompted us to reexamine this species throughout its range. Detailed comparison of the single specimen from Honduras with Costa Rican and Panamanian *C. gracilis* reveals that it represents a previously unrecognized species. Acquisition of two additional specimens of the new species during the course of our study confirms its distinctiveness. The purposes of this paper are to describe and illustrate this new small-eared shrew and to briefly document its relationship to other members of the genus *Cryptotis.*

Methods

All external and craniodental measurements reported herein are in millimeters (mm). External measurements of the holotype were taken by us on the fluid preserved specimen with the skull removed. External measurements of the two paratypes were taken by us on the fluid preserved specimens with the skulls in place; subsequently, we removed the skulls and all craniodental measurements were taken from cleaned skulls. Sixteen cranial measurements were taken to the nearest 0.1 mm using either a hand-held dial caliper or an ocular micrometer in a Wilde M50 binocular microscope (Table 1). Cranial measurements follow Choate (1970), in part, and mandibular measurements follow Jammot (1972), in part. All craniodental measurements are further diagrammed in a forthcoming manuscript by us on geographical variation in *C. gracilis.* Dental terminology follows Choate (1970). Capitalized color names are from Ridgeway (1912).

Multivariate analyses were carried out using the University of Kansas Academic Computing Services' IBM VM/CMS operating system. Discriminant function analysis (BMDP7M) was performed on 8 cranial and 7 mandibular measurements (Table 1; condylobasal length was not used because it was not measurable on all specimens) to discriminate among *C. gracilis* ($n = 20$), *C. nigrescens merriami* ($n = 13$), and *C. parva orophila* ($n = 16$). The holotype and one paratype of the new species were inserted into the discriminant function model as unknowns to evaluate their similarities to other species from the region. Because of their morphometrical similarity to *C. nigrescens merriami* based on the discriminant function analysis, principal components analysis (BMDP4M) was run using the same 15 variables. The holotype and one paratype of the new species and all specimens of *C. gracilis, C. nigrescens merriami,* and *C. parva orophila* were included in this analysis as a single population.

Specimens from the following institutions (followed by their acronyms) were examined in this study: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); University of Kansas Museum of Natural History, Lawrence (KU); Louisiana State University, Baton Rouge (LSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); National Museum of Natural History, Washington, D.C. (USNM).

Cryptotis hondurensis, new species

Figs. 1, 4B, 5B

Cryptotis gracilis.—Choate, 1970:282–285 [part].—Hall, 1981, 1:63–64 [part].

Holotype.—Skull of adult female with body preserved whole in alcohol, KU

106941; collected 5 Jul 1966 by William E. Duellman (collector number M-1405). Skull complete and unbroken; body intact, but with a patch of hair missing from venter.

The collection date is given in the original field catalog as 6 July 1966. However, the collector pointed out to us that this is probably the date he entered the specimen into his catalog. His original field notes indicate that the specimen was collected 5 July.

Paratypes.—(2): Skull of adult female with body preserved whole in alcohol, FMNH 86886; collected in the 1950s by Luis and Terua Williams. Skull lacking braincase; body intact.

Skull of juvenile male with body preserved whole in alcohol, UNAH (no number); collected 7 Feb 1988 by E. Frainvilledo (lot number 977). Skull lacking braincase and portions of palate and rostrum; body intact, but with a patch of hair missing from venter.

Type locality.—Honduras: Francisco Morazán Department; 12 km WNW of El Zamorano, W slope of Cerro Uyuca [=Cerro Oyuca; ca. 14°05′N, 87°06′W], 1680 m. The holotype was collected in pine forest (*Pinus pseudostrobus*) heavily laden with bromeliads; this region lies within the Lower Montane Moist Forest Life Zone of Holdridge (Organization of American States 1962).

Distribution.—Known only from pine and mixed pine and oak forests in highlands immediately east of Tegucigalpa; perhaps occurs throughout the Lower Montane Moist Forest Life Zone community or in high elevation pine forests in Honduras and possibly in neighboring areas of Guatemala, El Salvador, and Nicaragua.

Measurements of holotype.—Total length, ca. 84; tail, 29; hind foot, 12; ear, 6; condylobasal length, 19.2; palatal length, 8.4; maxillary breadth, 6.0; interorbital breadth, 4.3; maxillary toothrow, 7.1; cranial breadth, 9.2; mandibular toothrow, 5.5 (see Table 1).

Diagnosis.—A smaller species of the genus *Cryptotis* characterized by its similar dorsal and ventral coloration, a long and tapered tail, a long and narrow snout, a wide zygomatic plate, a complex M3, nearly perpendicular conformation of the junction of the coronoid process with the horizontal ramus, a short and broad articular process, and talonid of m3 with only a single cusp.

Description.—Size small for the genus (Table 1); tail long (ca. 42–53% of head and body length), tapering to a point; front feet and claws normal for genus, not enlarged; viewed ventrally, the snout is long and narrow; when air-dried the pelage of the fluid-preserved holotype is dense and soft, the dorsal guard hairs about 4 to 5 mm long; dorsal fur shows distinct banding, the proximal 75% of the guard hairs is pale gray in color, whereas the distal 25% is close to Prout's Brown; venter appears somewhat paler than dorsum. The overall brownish coloration of the specimen may be due to fading or bleaching. This color resembles some older, fluid-preserved specimens of *C. gracilis,* yet *C. gracilis* preserved as dried study skins are Fuscous to Chaetura Black.

Rostrum long, of medium breadth relative to other *Cryptotis* (Fig. 1); interorbital constriction of medium breadth; braincase low, flat; zygomatic plate long, anterior border aligned with mesostyle-metastyle valley of M1, posterior border aligned with posterior base of maxillary process and middle of M3; upper toothrow may be uncrowded, U4 aligned with toothrow and clearly visible in labial view (holotype—Fig. 4B) or crowded, U4 displaced medially and not clearly visible in labial view (both paratypes); P4, M1, M2 slightly recessed on posterior border; M3 with paracrista, precentrocrista, and short postcentrocrista, as well as well developed protocone, paracone, and metacone; dentition not particularly bulbous.

Mandible short, moderately broad for the genus (Fig. 1); coronoid process joins horizontal ramus at nearly a right angle; distance between coronoid process and posterior border of m3 is short; viewed posteriorly, articular process is short and narrow, with a broad ventral articular facet

Table 1.—Means (±*SD*) and observed ranges for skin, cranial, and mandibular measurements of Central American *Cryptotis* used in this study. Sample sizes (in parentheses) may be different for head and body length, tail length, and condylobasal length. The order of measurements of *C. hondurensis* is the holotype followed by the two paratypes. Missing measurements from the paratypes are represented by x.

C. hondurensis (holotype and 2 paratypes)	*C. gracilis* (*n* = 20)	*C. nigrescens merriami* (*n* = 13)	*C. parva orophila* (*n* = 16)
Head and body length			
55, 63, 64	73 ± 5 60–79 (*n* = 18)	69 ± 4 65–76	65 ± 7 58–77 (*n* = 11)
Tail length			
29, 27, 27	34 ± 3 30–41 (*n* = 18)	29 ± 3 24–33	21 ± 2 17–24 (*n* = 11)
Tail length (as % of head and body length)			
53, 43, 42	48 ± 5 38–58 (*n* = 18)	42 ± 5 32–50	33 ± 4 29–38 (*n* = 11)
Condylobasal length			
19.2, x, x	19.6 ± 0.5 18.7–20.4	19.4 ± 0.3 18.9–20.0 (*n* = 11)	17.1 ± 0.3 16.7–17.7 (*n* = 10)
Zygomatic plate length			
2.2, 2.0, 2.1	1.8 ± 0.1 1.5–2.0	2.3 ± 0.2 2.0–2.6	1.5 ± 0.1 1.4–1.8
Interorbital breadth			
4.3, 4.5, x	4.7 ± 0.2 4.1–5.2	4.8 ± 0.1 4.5–4.9	4.0 ± 0.1 3.8–4.4
U1–U1 breadth			
2.4, 2.4, x	2.4 ± 0.2 2.0–2.6	2.7 ± 0.1 2.4–2.8	2.4 ± 0.1 2.0–2.5
M2–M2 breadth			
5.4, 5.4, x	5.4 ± 0.3 5.0–5.8	5.9 ± 0.1 5.6–6.2	5.1 ± 0.2 4.9–5.5
Palatal length			
8.4, 7.8, x	8.8 ± 0.3 8.3–9.3	8.4 ± 0.2 8.1–8.8	7.2 ± 0.4 6.0–7.8
Maxillary toothrow length (U1–M3)			
7.1, 7.1, 7.1	7.6 ± 0.3 7.1–8.0	7.4 ± 0.1 7.1–7.5	6.2 ± 0.2 5.9–6.7
Unicuspid toothrow length			
2.6, 2.4, 2.4	2.6 ± 0.1 2.4–2.9	2.5 ± 0.1 2.3–2.6	2.0 ± 0.1 1.8–2.2
Posterior width of M1			
1.7, 1.7, 1.9	1.7 ± 0.1 1.6–1.8	1.9 ± 0.1 1.8–2.0	1.6 ± 0.1 1.6–1.8
Mandibular length (inferior sigmoid notch to mental foramen)			
6.1, 5.8, 6.3	6.4 ± 0.2 6.1–6.7	6.6 ± 0.2 6.3–6.8	5.4 ± 0.2 4.8–5.8

Table 1.—Continued.

C. hondurensis (holotype and 2 paratypes)	*C. gracilis* (*n* = 20)	*C. nigrescens merriami* (*n* = 13)	*C. parva orophila* (*n* = 16)
Coronoid process height			
4.8, 4.4, 4.6	4.1 ± 0.2	5.1 ± 0.2	4.1 ± 0.2
	3.7–4.4	4.8–5.3	3.7–4.3
Articular condyle height			
3.6, 3.6, 3.8	3.7 ± 0.2	3.8–0.2	3.4 ± 0.1
	3.3–4.0	3.6–4.3	3.2–3.7
Distance from articular condyle to m3			
4.3, 4.3, 4.4	5.1 ± 0.2	4.7 ± 0.1	4.1 ± 0.1
	4.8–5.3	4.5–4.9	4.0–4.3
Articular condyle breadth			
3.0, 2.8, 2.8	3.0 ± 0.1	3.1 ± 0.1	2.6 ± 0.1
	2.7–3.1	3.0–3.2	2.4–2.7
Mandibular toothrow (p3–m3) length			
5.5, 5.3, 5.7	6.0 ± 0.2	5.7 ± 0.1	4.9 ± 0.2
	5.6–6.3	5.4–5.9	4.7–5.3
ml length			
1.7, 1.7, 1.7	1.7 ± 0.1	1.8 ± 0.2	1.5 ± 0.1
	1.5–1.8	1.7–1.9	1.3–1.6

(Fig. 5B); lower sigmoid notch shallow; upper sigmoid notch rounded; posterior border of lower incisor extends posterior to the cusps of p4; talonid of m3 consists of hypoconid only.

Comparisons.—*Cryptotis hondurensis* resembles *C. gracilis* in its long tail, the complexity of the cusps of M3, and in some general external and cranial features, which account for its previous allocation to the latter species. However, it is much closer in many other features to *C. nigrescens merriami,* to which it may be most closely related phylogenetically. It differs from *C. gracilis, C. nigrescens merriami,* and *C. parva orophila* in the following:

Cryptotis gracilis (Figs. 2, 4A, 5A): *Cryptotis hondurensis* has shorter (4–5 mm vs. 6–7 mm), less woolly dorsal pelage; a shorter, broader rostrum that is not as highly arched; narrower braincase; narrower interorbital constriction; longer zygomatic plate; relatively shorter maxillary toothrow; P4 almost quadrate; M1 shorter and broader; paracone and metacone of M3 closer together; coronoid process absolutely higher, joining horizontal ramus at nearly a right angle; shorter distance between coronoid process and m3; shorter mandibular toothrow; shorter, broader articular process, with much broader ventral articulating surface; shallower lower sigmoid notch; posterior margin of lower incisor extends posterior to cusps of p4; broader and more massive m1 and m2; talonid of m3 consists of only hypoconid.

Cryptotis parva orophila: *Cryptotis hondurensis* is larger and has a longer tail relative to body; longer (4–5 mm vs. 3–4 mm), silkier dorsal pelage; longer, narrower rostrum; lower, flatter braincase; P4, M1, M2 not as deeply recessed posteriorly; M3 with paracrista, precentrocrista, postcentrocrista, and well developed paracone and metacone; narrower articular process of mandible, with much broader ventral articulating surface.

Cryptotis nigrescens merriami (Figs. 3, 4C, 5C): *Cryptotis hondurensis* has a longer, narrower tail, tapering to a point at its tip rather

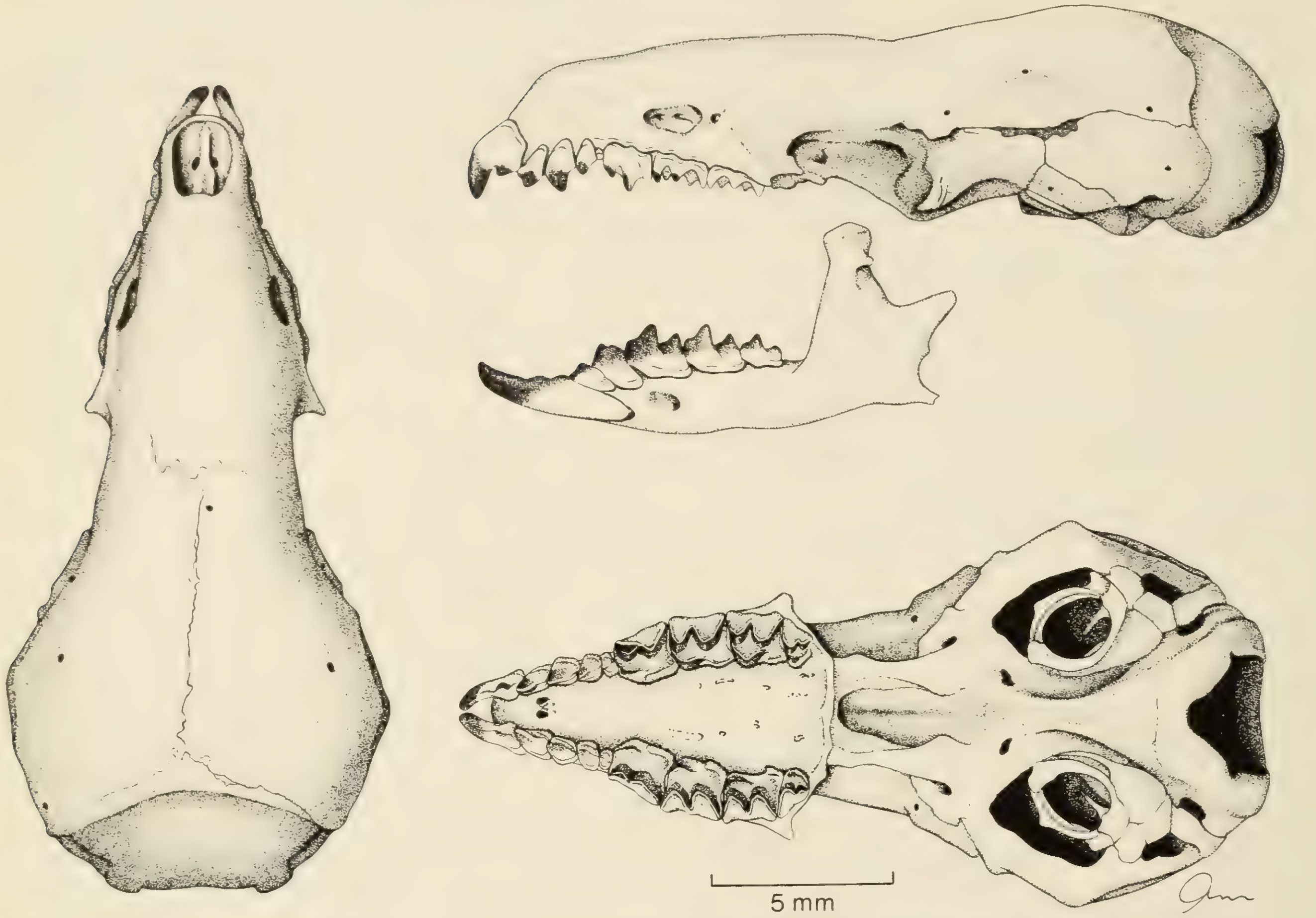

Fig. 1. Dorsal and ventral view of the skull and lateral views of the skull and mandible of the holotype of *C. hondurensis* (KU 106941).

than being thick and rounded as in *C. nigrescens merriami*; relatively longer, narrower rostrum; much narrower palate; lower, flatter braincase; less massive upper and lower molars and upper unicuspids; M3 with paracrista, precentrocrista, postcentrocrista, and well developed paracone and metacone; teeth not bulbous; smaller and narrower articular process of mandible.

Etymology.—The specific epithet *hondurensis* is derived from Honduras, the country of origin of the holotype and both paratypes.

Multivariate Analyses

Discriminant function analysis yielded a numerical model that required four measurements to discriminate among the three species: palatal length, coronoid process height, distance from articular condyle to posterior of m3, and zygomatic plate breadth. All specimens of *C. gracilis, C. nigrescens,* and *C. parva* were correctly classified into their predetermined groups. The holotype and paratype of *C. hondurensis* are clearly distinct from *C. gracilis* and are closest to *C. nigrescens merriami* in general cranial shape and size, as can be seen in a plot of specimens on canonical axes 1 and 2 (Fig. 6).

Principal components analysis revealed clear distinctions among the four taxa, separating without overlap all specimens of *C. gracilis, C. nigrescens,* and *C. parva,* and showing *C. hondurensis* intermediate amongst them on factor axes 1 and 2 (Fig. 7). In this model, Factor 1 is clearly a size axis and Factor 2 is a shape axis contrasting a group of variables representing mandibular height and palatal width (coronoid process height, posterior width of M1, U1–U1 breadth, zygomatic plate breadth, and M2–M2 breadth) with a second group of variables representing mandibular and palatal lengths (articular condyle to m3 distance,

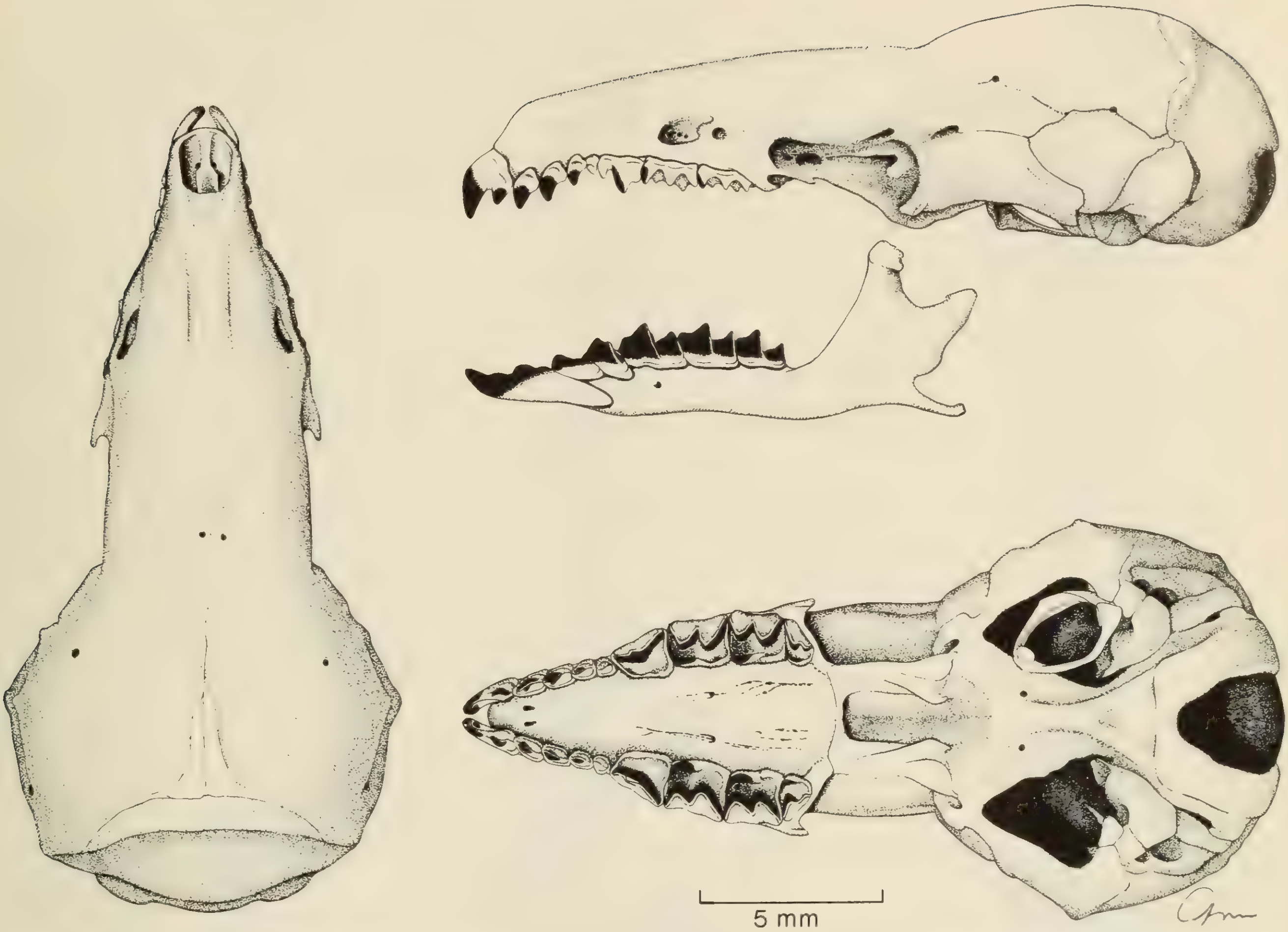

Fig. 2. Dorsal and ventral view of the skull and lateral views of the skull and mandible of *C. gracilis* (LSU 12659).

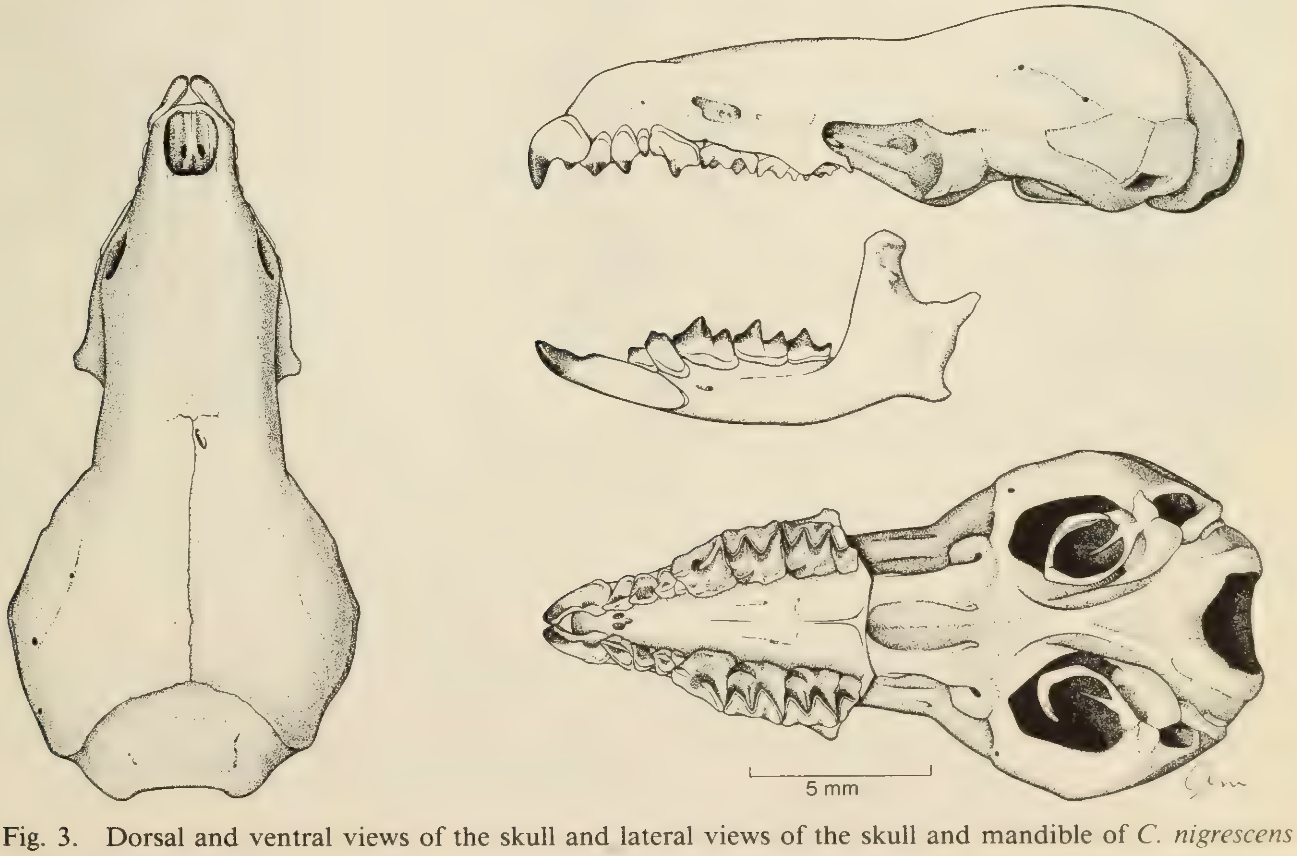

Fig. 3. Dorsal and ventral views of the skull and lateral views of the skull and mandible of *C. nigrescens merriami* (MVZ 130335).

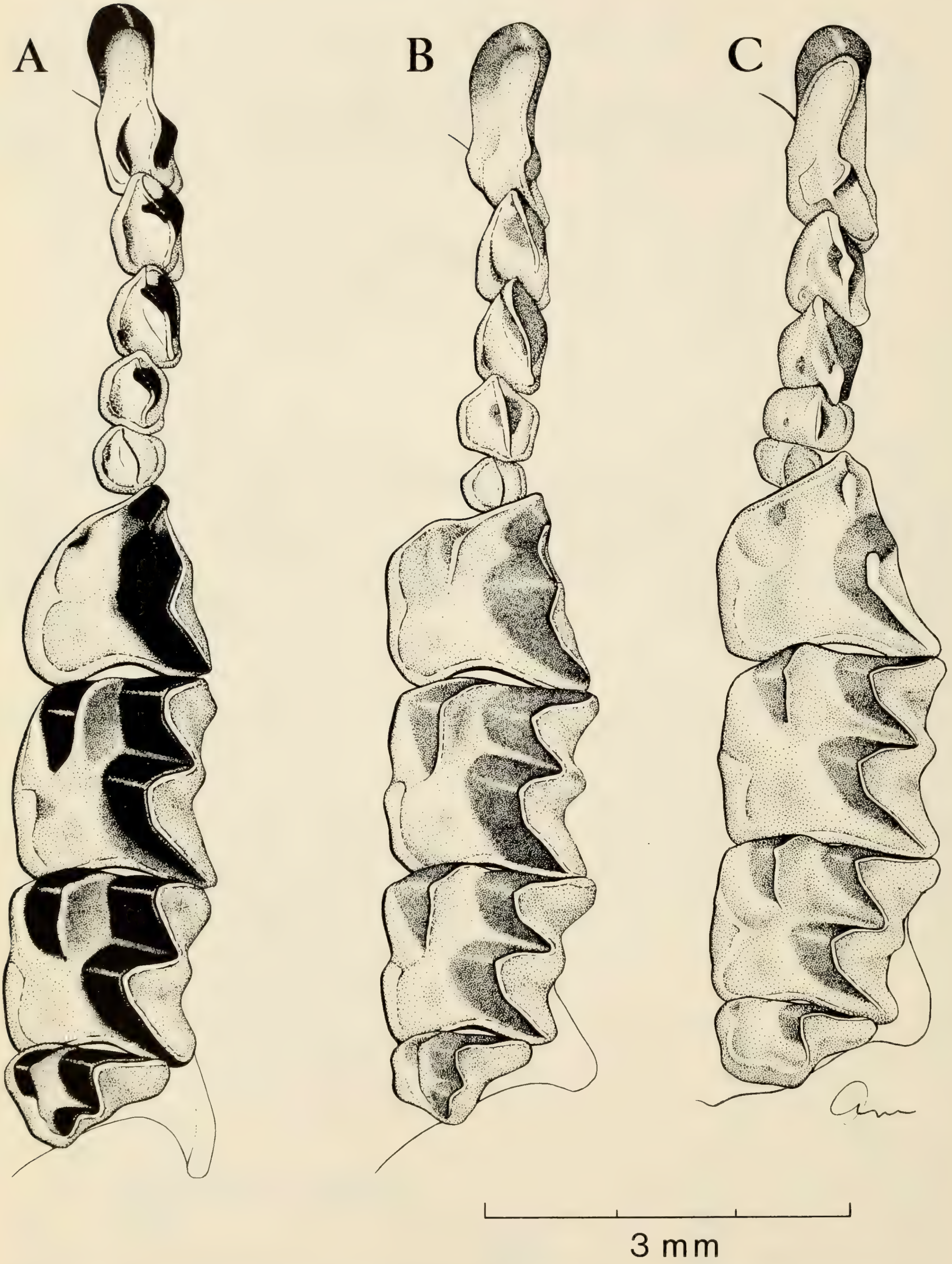

Fig. 4. Left maxillary toothrows of *C. gracilis* (A), *C. hondurensis* (B), and *C. nigrescens merriami* (C).

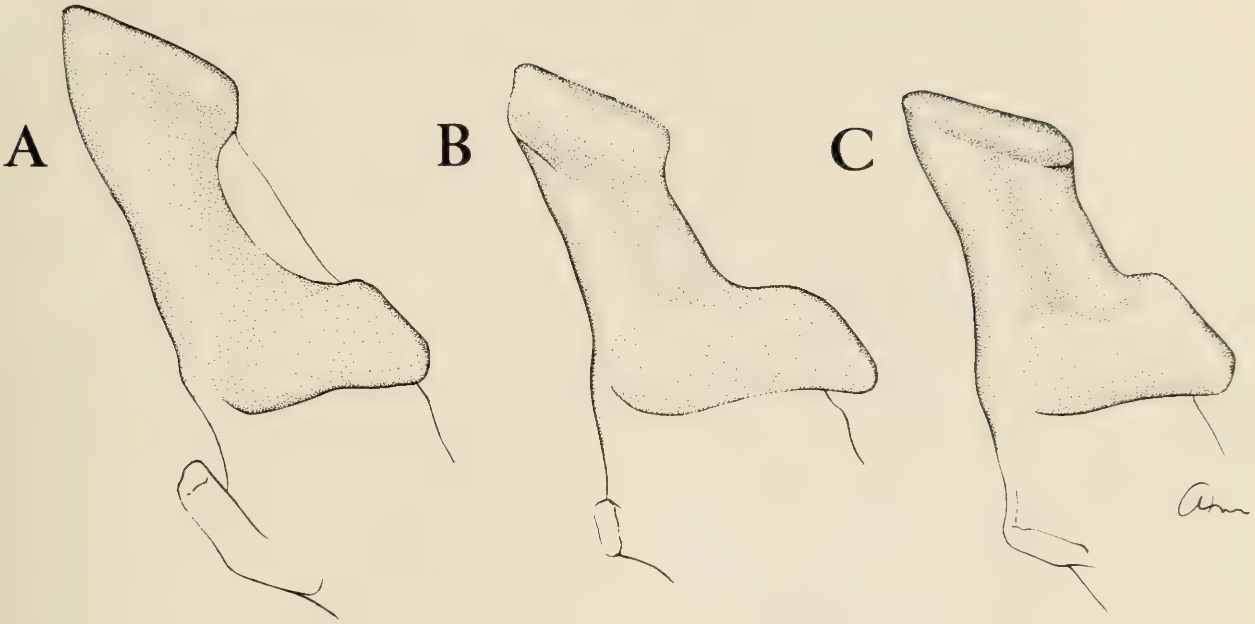

Fig. 5. Left mandibular articular condyles of *C. gracilis* (A), *C. hondurensis* (B), and *C. nigrescens merriami* (C).

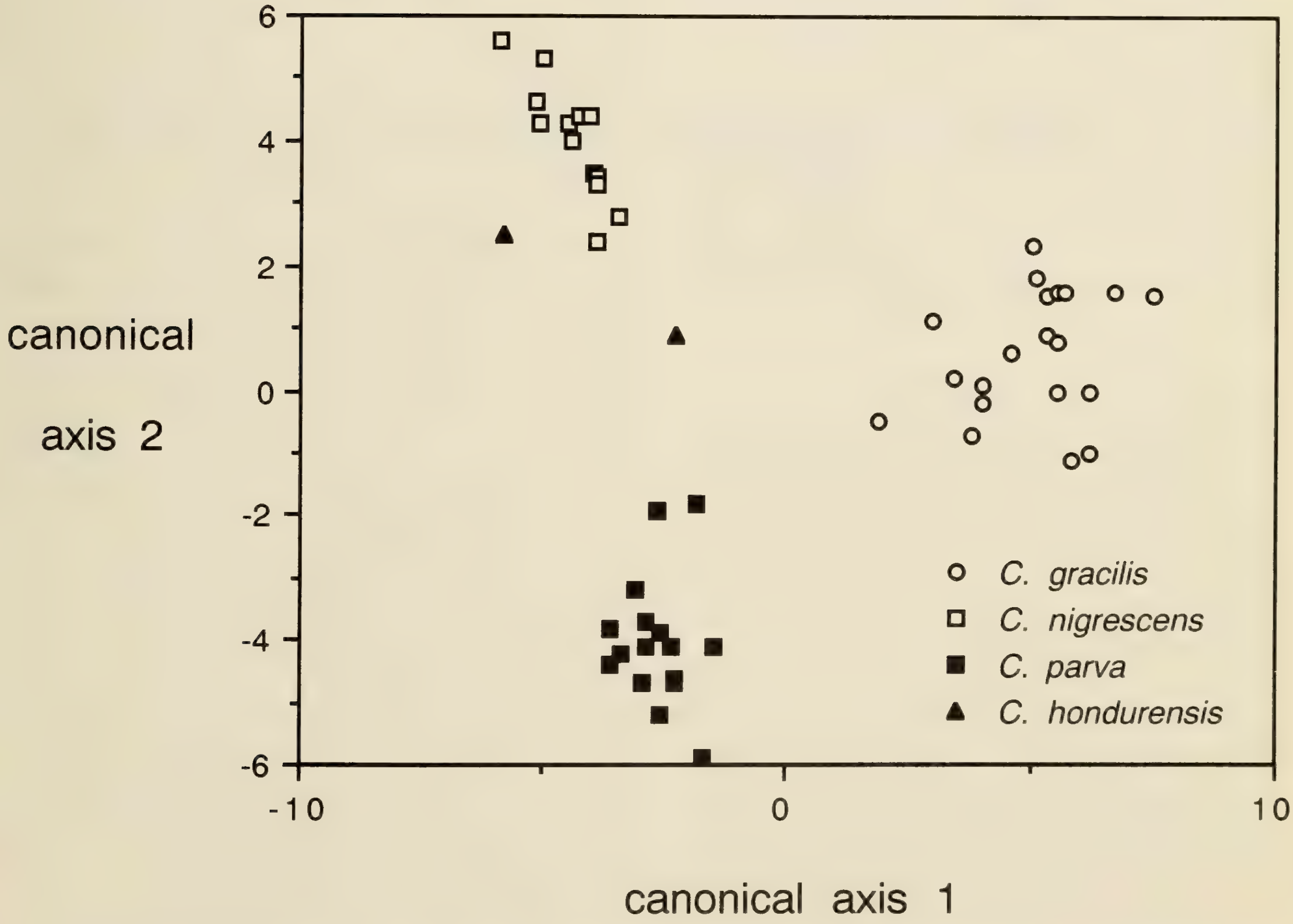

Fig. 6. Plot of specimens of *C. gracilis, C. nigrescens merriami,* and *C. parva orophila* and the holotype and one paratype of *C. hondurensis* on canonical axes 1 and 2.

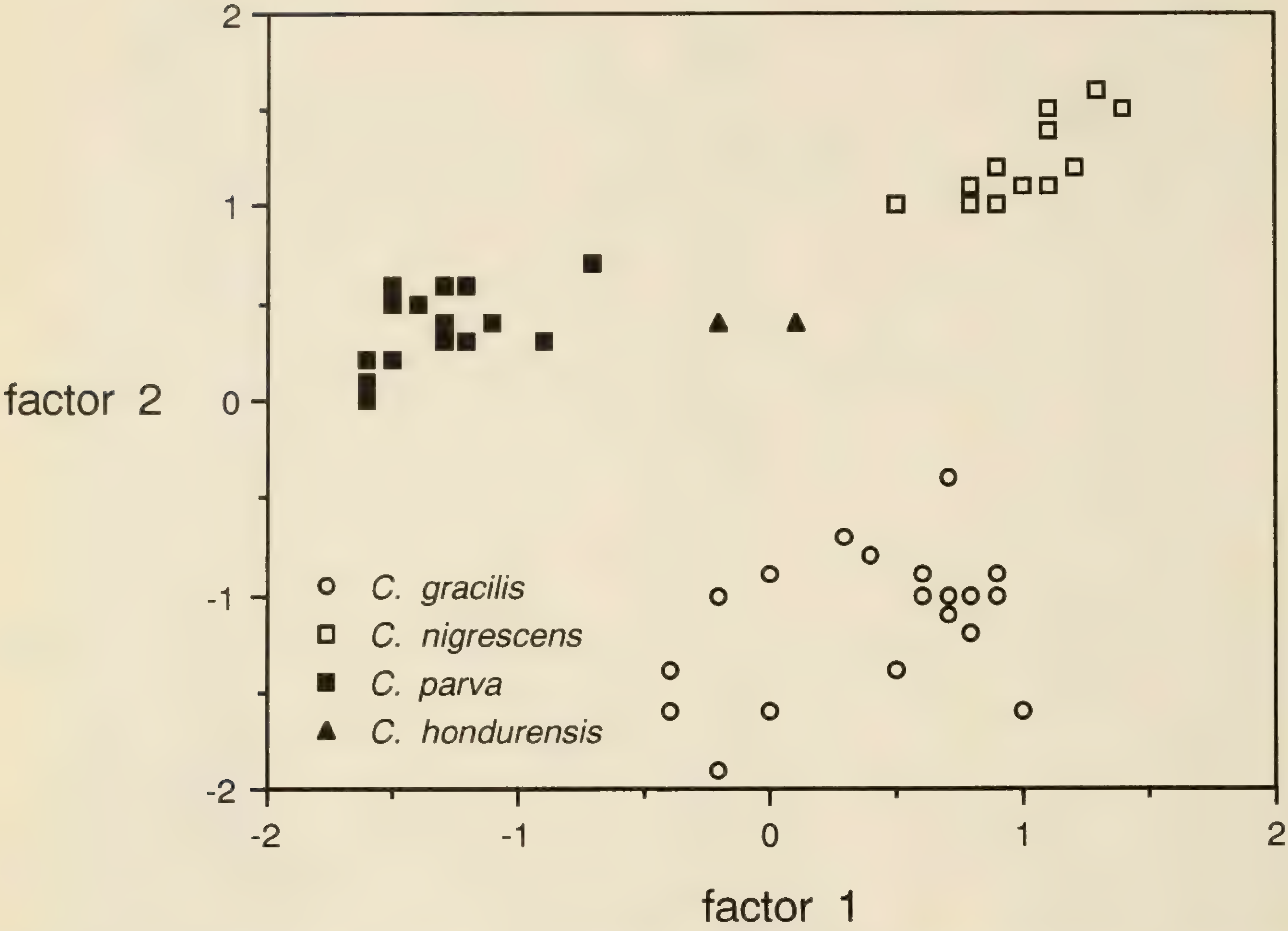

Fig. 7. Plot of specimens of *C. gracilis, C. nigrescens merriami,* and *C. parva orophila* and the holotype and one paratype of *C. hondurensis* on principal components factor axes 1 and 2.

palatal length, unicuspid toothrow, mandibular toothrow, and maxillary toothrow).

Discussion

Choate (1970:284) first noted some of the differences between the Honduran specimen and Costa Rican *C. gracilis*: "the specimen from Honduras differs from typical Costa Rican individuals in being slightly smaller, both externally and cranially, and in having only one cusp (the hypoconid) as opposed to both hypoconid and entoconid on the talonid of m3." Although the crania of *C. hondurensis* and *C. gracilis* appear similar in general aspect, important differences exist, particularly in the shape of the rostrum and the breadth of the zygomatic plate. In addition, the mandibles of the two species are quite distinct (Figs. 1, 2). *Cryptotis gracilis* has a long, narrow, mandibular ramus with small teeth and an uncrowded toothrow. The coronoid process has a wide base that attaches to the ramus at a low angle. The shape and angle of the coronoid process in *C. gracilis* is unlike any Recent or fossil Holarctic soricid we have studied and instead allies *C. gracilis* with certain Central American and South American species. In contrast, *C. hondurensis* has a mandible more typical of the family: short and broad, with the coronoid process joined to the horizontal ramus at a nearly right angle. The mandibular articular process of *C. hondurensis* is similar to that of *C. nigrescens,* but the lower articulation is relatively much broader in *C. hondurensis* than in other species of *Cryptotis* we have studied.

Among species of *Cryptotis* the M3 is highly variable in size and coronal complexity. Choate (1970) indicated that, in the primitive condition, the tooth is relatively large with paracrista, paracone, precentrocrista, postcentrocrista, metacone, and metacrista. In more specialized grades, M3 becomes successively shortened posteriorly, with resulting diminution and loss of the more posterior and lingual structures (Choate 1970). If this character polarity is true, then the M3 of *C. hondurensis*, like that of *C. gracilis*, is rather primitive for the genus. *Cryptotis hondurensis* possesses both paracone and metacone on M3 but, unlike *C. gracilis*, these structures are close together and the mesostyle does not extend very far labially (Fig. 4A, B).

Using keys to North and Middle American *Cryptotis* provided by Choate (1970) and Hall (1981), *C. hondurensis* would be identified as *C. gracilis* in couplet 2′. However, the two species can be separated readily on the basis of the contrasting characters described above.

The Honduran specimen referred to *C. gracilis* by Choate (1970) represented the only known example of *C. gracilis* from north of Costa Rica. Our recognition of this animal as a distinct species restricts the known range of *C. gracilis* to the Talamancan and Tilarán highlands of Costa Rica and the adjacent Chiriquí highlands of extreme western Panama.

Acknowledgments

We thank William E. Duellman, whose field efforts provided the specimen described herein as the holotype of *C. hondurensis* and who generously provided additional information regarding the collection of this specimen. Anne M. Musser skillfully executed the illustrations. We are grateful to Thor Holmes for his expertise in specimen preparation, Cara Burres for help with computer graphics, and Norman A. Slade and Marianna D. Wood for advice in using multivariate statistics. Michael D. Carleton, Alfred L. Gardner, Robert S. Hoffmann, Thor Holmes, and Norman A. Slade critiqued earlier versions of this manuscript, providing comments that improved it substantially. Gloria Arratia aided with the translation of our abstract. Additionally, we thank the following curators for loans of specimens under their care at their respective institutions: Guy G. Musser (AMNH), Bruce D. Patterson (FMNH), Mark S. Hafner (LSU), James L. Patton and Barbara R. Stein (MVZ), Phil Myers (UMMZ), Gustavo A. Cruz and B. Myton (UNAH), and Michael D. Carleton and Alfred L. Gardner (USNM). Mark S. Hafner graciously allowed us to illustrate one of the LSU specimens of *C. gracilis*, and James L. Patton similarly permitted us to illustrate a MVZ specimen of *C. nigrescens merriami*. Bruce D. Patterson and Gustavo A. Cruz kindly allowed us to remove skulls from fluid preserved specimens of the paratypes under their respective care. Timothy McCarthy brought the UNAH paratype to our attention and made it available to us. Funding for this project was provided by a grant to Timm from the University of Kansas General Research Fund.

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Appendix
Specimens Examined

Cryptotis gracilis (20). Costa Rica: Cartago: Volcán Irazú, Finca Coliblanco, 2350 m (2 UMMZ); Volcán Irazú, 0.25 mi N of San Juan Chicoa, 2860 m (1 UMMZ); Volcán Irazú, 2500 m (1 KU); Volcán Turrialba, Hacienda El Retiro, 2590 m (4 UMMZ). San José: Cerro Chirripó, Headwaters of Río Talari, 11,600 ft (4 LSU); Cerro de la Muerte, Hotel Georgina, 3100 m (1 USNM); La Piedra, ca. 4 mi SW Cerro Chirripó, 10,500 ft (4 LSU); Las Vueltas, 8000 ft (1 UMMZ). Panama: Bocas del Toro: Cerro Fabrega, 8400 ft (1 USNM). Chiriquí: Cerro Punta, Boquete Trail, 7600 ft (1 USNM).

C. hondurensis (3). Honduras: Francisco Morazán: Cerro Uyuca (1 KU—holotype); near San Juancito mines, 1700 m (1 FMNH); La Rosario, San Juancito, La Tigra National Park (1 UNAH).

C. nigrescens merriami (13). El Salvador: Morazán: Mount Cacaguatique, 3800–4700 ft (2 MVZ). San Miguel: Mount Cacaguatique, 3500–4000 ft (7 MVZ, 2 UMMZ). Guatemala: Alta Verapaz: Tucuru, Hacienda Concepción, 1100 m (1 UMMZ). Huehuetenango: Barillas, Hacienda Santa Gregoria (1 UMMZ).

C. parva orophila (16). Costa Rica: Alajuela: Zarcero, 6000 ft (1 FMNH); Cartago: Cartago (2 UMMZ); Cerro Tablazo, 1983 m (1 USNM); La Estrella (1 AMNH). Heredia: Barva, San José de la Montaña, Paso Llano, 1800 m (3 KU); Barva, San Miguel de la Montaña, 1690–1700 m (3 KU). San José: 10 mi S. of Cartago, El Muñeco, 3800 ft (1 UMMZ); San Rafael de Montes de Oca, 4300 ft (1 KU); Santa Ana (1 LSU). Nicaragua: Jinotega: 12 km S. of Jinotega, 1400 m (1 KU). Matagalpa: 9 mi N. of Matagalpa, Santa María de Ostuma, 1300 m (1 UMMZ).

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A NEW SPECIES OF *OCADIA* (TESTUDINES: BATAGURIDAE) FROM HAINAN ISLAND, CHINA

William P. McCord and John B. Iverson

Abstract.—A new species of batagurine turtle, *Ocadia philippeni,* is described from Hainan Island, China. Similar to and sympatric with *Ocadia sinensis,* it differs from that species by having fewer broad neck stripes, a ventral pinkish-orange wash, a wider plastron, a relatively shorter interfemoral seam and bridge, and a relatively longer gular scute.

Originally described by Gray (1834) as *Emys sinensis,* the Chinese stripe-necked turtle was placed in the monotypic genus *Ocadia* by the same author in 1870. All subsequent authors have recognized *Ocadia* as a monotypic genus (see Wermuth & Mertens 1977). *Ocadia sinensis* is known from Taiwan, Hainan Island, and on the Asian mainland from southeastern China to central Vietnam (Iverson 1986). No extant subspecies have been described, although Taiwan specimens have more faded plastral blotches than those from other locations (Pritchard 1979). Tao (1988) described *O. sinensis changwui* from a single partial carapace found in late Pleistocene sediments off the west coast of Taiwan. However, the diagnosis used highly variable carapacial scute shape characters; hence, the validity of this fossil taxon awaits a comparison with additional fossil and recent osteological material.

Over the past two years Mr. Oscar Shiu sent McCord a series of distinct stripe-necked batagurine turtles from China. These turtles apparently were found sympatrically with *Ocadia sinensis* and are more similar to that species than to any other Chinese turtle. They are described herein as the second species of the genus *Ocadia,* even though skeletal material is not yet available for definitive generic placement (e.g., McDowell 1964, Hirayama 1984, Gaffney & Meylan 1988).

In honor of Hans-Dieter Philippen, we name this distinctive species

Ocadia philippeni, new species
Philippen's stripe-necked turtle
Fig. 1c, d

Holotype.—UF #80766, an adult female, preserved in alcohol; reported to have been collected near Kancheng [18°51′N, 108°37′E; =48 km from Tungfang (19°03′N, 108°56′E)], western Hainan Island, China; purchased from local people by Mr. Oscar Shiu, in the spring of 1988 or 1989.

Paratype.—UF #80765, a juvenile male, preserved in alcohol; same data as holotype.

Diagnosis.—A large species of *Ocadia* (Table 1) with a moderately tricarinate carapace with the anterior neural bones anteriorly short-sided; an unhinged plastron; four yellow, black-bordered lateral head and neck stripes separated by narrow brown stripes (at least eight black-bordered, narrow, cream to yellow stripes in *O. sinensis*); ventral surfaces of shell and skin washed with pinkish-orange even in adults (cream to yellow in *O. sinensis*); a relatively short bridge and broad plastron (bridge length usually less than 90% of anterior width of plastral hindlobe in *O. philippeni*; more than 80% in *O.*

Table 1.—Morphometric characters useful in discriminating among species of the genus *Ocadia*. Character abbreviations are interfemoral seam length (IF), maximum gular scute length (GL), bridge length (BL), and anterior width of plastral hindlobe (PW3). Values are means followed by range in parentheses.

Sample	Sex	*n*	Carapace length (mm)	IF/GL	IF/PW3
O. philippeni					
Hainan	M	7	169.0 (113–199)	1.01 (0.72–1.43)	0.31 (0.26–0.41)
	F	2	216.7 (214–219)	1.18 (1.16–1.20)	0.33 (0.33–0.33)
O. sinensis					
Hainan	M	9	125.3 (107–155)	1.48 (1.08–1.80)	0.43 (0.39–0.47)
	F	7	146.8 (114–220)	1.31 (1.09–1.47)	0.37 (0.34–0.42)
Taiwan	M	4	177.7 (155–200)	1.32 (1.13–1.56)	0.39 (0.31–0.45)
	F	9	201.0 (176–235)	1.33 (1.15–1.60)	0.38 (0.33–0.45)
China	M	2	133.5 (117–150)	1.56 (1.51–1.60)	0.43 (0.39–0.47)
	F	2	261.0 (251–271)	1.52 (1.47–1.56)	0.42 (0.37–0.47)
Vietnam/Laos	M	4	180.1 (136–245)	1.62 (1.40–2.04)	0.42 (0.38–0.46)
	F	5	188.8 (116–258)	1.39 (1.18–1.68)	0.40 (0.36–0.43)
Total	M	19	143.4 (107–200)	1.48 (1.08–2.04)	0.42 (0.31–0.47)
	F	23	187.0 (114–271)	1.35 (1.09–1.68)	0.38 (0.33–0.47)

sinensis); and a relatively short interfemoral seam and long gular scute (interfemoral seam length usually less than 120% of maximum gular length in *O. philippeni*; more than 110% in *O. sinensis*) (Fig. 2).

Description (based on two adult females, six adult males, and one juvenile male, including the types).—Carapace length (CL) to at least 199 mm in males and at least 219 mm in females, elliptical, moderately tricarinate and domed (maximum shell height/CL = 0.355 to 0.402; mean = 0.369), widest at the level of marginal (M) 8 (maximum carapace width/CL = 0.685 to 0.762; mean = 0.720), with a smooth to slightly serrated posterior margin, and with moderately obvious growth annuli. M1, 7, 8, and 9 largest, approximately coequal in length; M11 smallest; M4, 8, or 9 tallest; M8–11 distinctly flared. Cervical scute small, generally rectangular, but wider posteriorly than anteriorly, and longer than wide. Vertebrals (V) 2–5 wider than long; V1 variable in relative length versus width, but not contacting seam between M1 and M2; V5 usually not contacting M10. Medial keel least pronounced on V5; weaker lateral keels most pronounced on costals C2 and C3. Carapace rusty brown to nearly black; if brown, carinae marked with dark brown to black. A black blotch on ventral posterolateral quadrant of each marginal, although sometimes blotch covers nearly half of the ventral surface of each marginal.

Maximum plastron length shorter than carapace length (PL/CL = 0.96–1.00 in females; 0.90 to 0.94 in males). Plastron slightly upturned anteriorly, with no hinge present. Plastral forelobe width (PW1) at level of junction of humeropectoral seam and lateral plastral margin 40.0% (range 39 to 43%) of carapace length. Anterior width of plastral hindlobe (PW3: at lateral junction of abdominofemoral seam) 44.9% (range 43 to 46%) of carapace length. Plastral hindlobe with relatively deep anal notch (medial depth of notch averages 53% of interanal seam length; range 31 to 105%). Bridge moderately long (bridge length/CL = 0.32 to 0.40, mean = 0.35; BL/PW3 = 0.73 to 0.88, mean = 0.78); single large axillary and inguinal scutes on each bridge.

Table 1.—Extended.

GL/BL	BL/PW3
0.41 (0.36–0.49)	0.76 (0.73–0.81)
0.32 (0.31–0.33)	0.88 (0.87–0.88)
0.33 (0.26–0.40)	0.89 (0.84–0.95)
0.33 (0.29–0.35)	0.88 (0.85–0.94)
0.35 (0.32–0.39)	0.85 (0.79–0.91)
0.31 (0.25–0.34)	0.92 (0.88–0.96)
0.28 (0.28–0.29)	0.98 (0.92–1.03)
0.30 (0.28–0.31)	0.92 (0.88–0.96)
0.32 (0.26–0.36)	0.83 (0.79–0.86)
0.34 (0.30–0.36)	0.86 (0.79–0.93)
0.33 (0.26–0.40)	0.88 (0.79–1.03)
0.32 (0.25–0.36)	0.90 (0.79–0.96)

Average plastral formula: interabdominal seam (IAB) > interpectoral seam (IP) ≫ interfemoral seam (IF) ≥ intergular seam (IG) > interanal seam (IAN) > interhumeral seam (IH). Interfemoral seam length/maximum gular length = 1.05 (0.72 to 1.43). Plastron pink to orange (Fig. 1), with a large (covering up to 50% of scute), black blotch on older portion of each scute (nearly completely faded on the humerals, pectorals, and abdominals in one specimen). A smaller black blotch also occurs on the bridge area of the pectoral and abdominal scutes, and occasionally on the axillary and inguinal scutes.

Head narrow; upper jaw unhooked; triturating surfaces of medium width, without ridges. Small tubercles evident between angle of jaw and tympanum. Dorsum uniform olive green to olive brown. Four narrow longitudinal black-bordered yellow stripes on side of head, separated by narrow brown or olive stripes. Dorsal-most stripe incomplete anteriorly. Middle two stripes originating at eye; upper one passing dorsal to tympanum and lower one passing across tympanum. Ventral-most stripe originating at angle of jaw. All stripes except most dorsal extending to base of neck. Chin yellow, with or without two small concentric black circles, but with seven black-bordered longitudinal stripes (often discontinuous) extending from level of tympanum to base of neck. Tomia flecked with black. Black horizontal line across eye (through pupil); iris yellow-green.

Anterior surface of antebrachium covered with large, imbricate scales, the largest 3 of which are sickle-shaped; largest scales on hindlimb at heel, but much smaller than largest forelimb scales. Upper parts of limbs and tail finely scaled. Exposed parts of forelimbs salmon to orange and heavily mottled with olive, brown, and/or black; a narrow, black-bordered salmon to orange stripe runs along anterior margin of forelimb to foot. Exposed parts of hindlimbs olive-green to brown to black dorsally and salmon ventrally; posterolateral margins with longitudinal black stripes. Recessed areas of skin salmon (usually) to orange to yellow. Tail relatively long, black dorsally, with a pair of longitudinal dorsolateral brown stripes extending from base of tail at least halfway to end of tail. Ventral tail pink or orange, with little to much black mottling, concentrated around the anus.

Males with a slightly concave plastron; females with a flat or convex plastron. Males with longer tails than females; vent at or beyond level of posterior carapace margin in males; anterior to it in females.

Other material.—One adult female and six adult males (all topotypic); alive in the collection of William P. McCord (WPM 1–7); to be deposited on death in the UF collection.

Distribution.—Known only from "near Kancheng." The precise locality could not be determined since the turtles were collected by local people.

Natural history.—Oscar Shiu reports that carapace length exceeds 36 cm and individuals reach 2.7 kg in mass. In captivity a

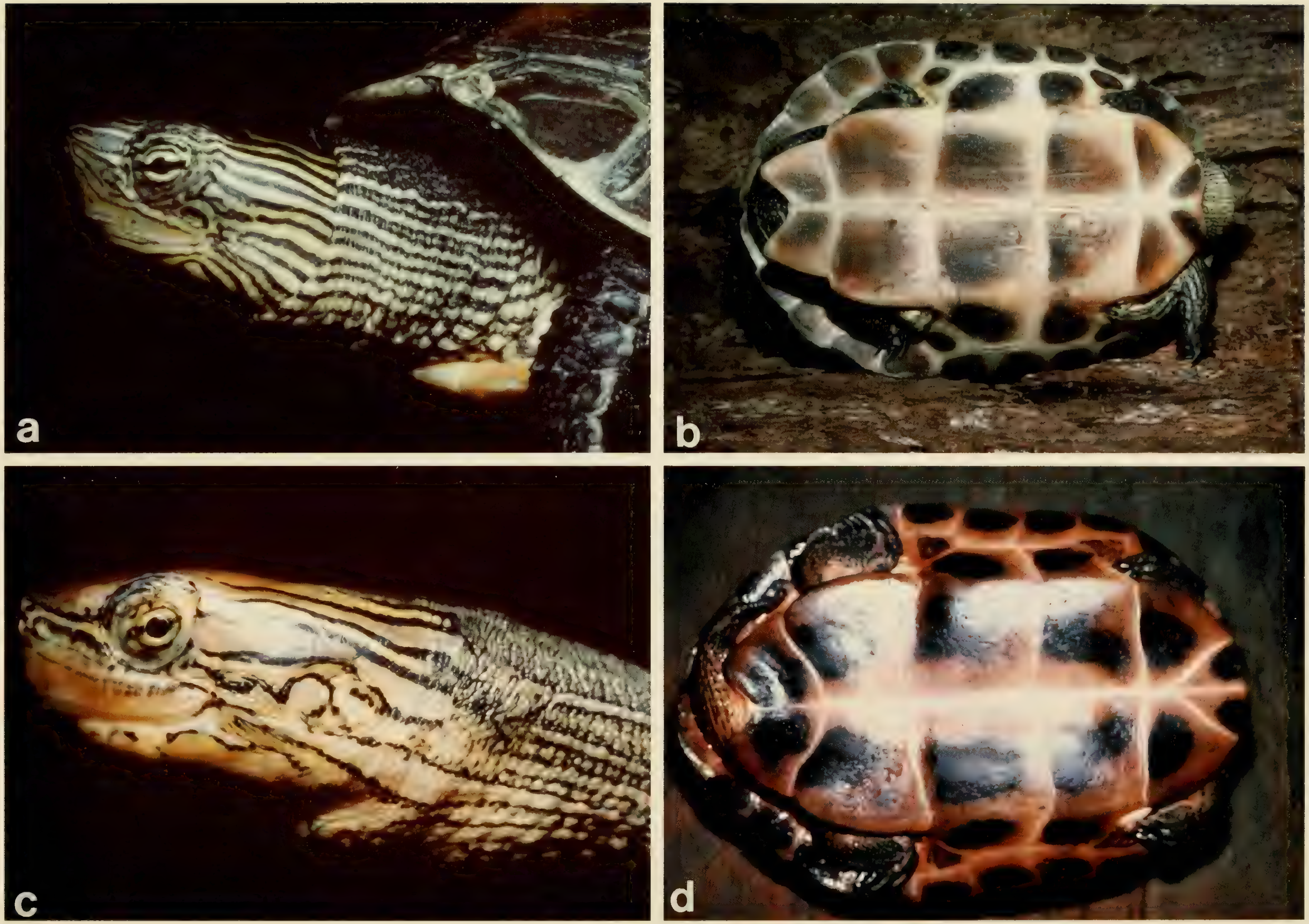

Fig. 1. Comparison of head patterns and plastra of male *Ocadia sinensis* (a, b) and *O. philippeni* new species (c, d; 199 mm carapace length; specimen alive in WPM collection).

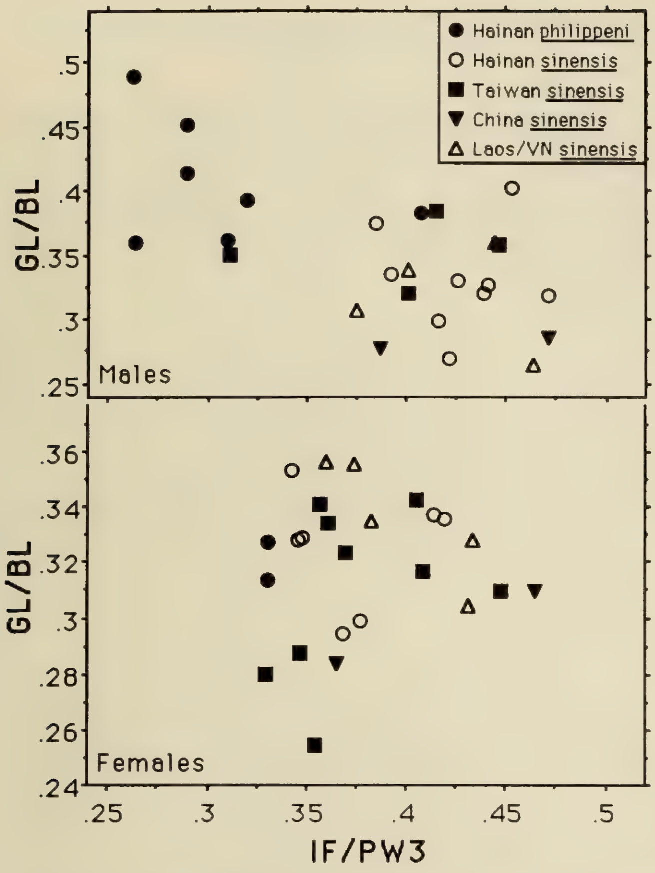

Fig. 2. Bivariate plot of the relationships among male (top) and female populations of the species of the genus *Ocadia* based on the characters IF/PW3 (interfemoral seam length/anterior width of plastral hindlobe) and GL/BL (maximum gular length/bridge length).

topotypic female (214 mm carapace length) laid six brittle-shelled, oblong eggs (mean length = 39.76 mm, range 38.7–41.6; mean width = 24.53 mm, range 24.0–25.2) in late October 1989.

Specimens examined.—(see Acknowledgments for acronyms) *Ocadia sinensis:* Laos (UF 80817–19 [3 specs]; WPM 1, alive), North Vietnam (MCZ 21051; UF uncatalogued [1 spec]; WPM 1–3, alive), Taiwan (FMNH 121230–32, 127172–73, 127175–78, 127180, 195492, 199750–51), China, Hainan Island (AMNH 30173, 30176–78, 30183–84, 30186–91, 30193, 30195–96; FMNH 6613 [formerly AMNH 30194]; MCZ 20687; MVZ 23940; UF 80816 [1 skeleton]), and China, mainland (BMNH 1947.3.5.26 [holotype]; MVZ 23943; WPM 1–2, alive). *Ocadia philippeni:* China, Hainan Island (UF 80765–66 [types]; WPM 1–7, alive).

Acknowledgments

This species would not have been collected without the efforts of Oscar Shiu of Hong Kong. Curators and collection managers at the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology at Harvard (MCZ), the Museum of Vertebrate Zoology at Berkeley (MVZ), the Florida Museum of Natural History (UF), and the United States National Museum (USNM) facilitated specimen loans. David L. Auth, Carl H. Ernst, and George R. Zug provided literature, pertinent information and/or other courtesies. Support for Iverson was provided by Earlham College, the Joseph Moore Museum of Natural History, and his family.

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BOEHLKENCHELYS LONGIDENTATA, A NEW GENUS AND SPECIES OF CHLOPSID EEL (TELEOSTEI: ANGUILLIFORMES) FROM THE INDO-WEST PACIFIC REGION

Kenneth A. Tighe

Abstract.—*Boehlkenchelys longidentata,* a new genus and species belonging to the family Chlopsidae, is described from the Indo-West Pacific. The genus and species is unique in the combination of the presence of a pectoral fin, uniserial vomerine dentition, high preopercular-mandibular pore counts and lateral position of posterior nostril.

The most recent reviews of the family Chlopsidae were those of Böhlke & Smith (1968), and Smith (1989). Böhlke & Smith (1968) recognized seven genera, while Smith (1989) described a new genus, bringing the total to eight. Recent collecting in the Fiji Islands and the Chagos Archipelago yielded six specimens of an undescribed species of eel that clearly belongs in this family, but does not fit in any of the nominal genera. Several additional specimens had been located in the collections of the Bishop Museum by the late James Böhlke, and were under study by him at the time of his death.

Methods and Materials

General methods for morphometric and meristic data for this study are given in Böhlke (1989). All measurements are given as a proportion of the total length (TL) except for subunits of the head which are presented as proportions of the head length (HL). Vertebral and fin ray counts were taken from radiographs. Total vertebral counts are of all elements including the hypural plate. Preanal and predorsal vertebral counts were taken using the definitions of Böhlke (1982). Precaudal vertebral counts include all elements up to the first vertebra with a distinct, posteriorly directed haemal spine. Meristic and morphometric data for the type series are presented with the values of the holotype first and the range of values of the paratypes given in brackets. The specimens are deposited at the Royal Ontario Museum (ROM), the Bernice P. Bishop Museum (BPBM), the National Museum of Natural History (USNM) and the Academy of Natural Sciences, Philadelphia (ANSP).

Boehlkenchelys, new genus

Diagnosis.—Distinguished from all other chlopsid genera by the following combination of characters: vomerine teeth in a single, irregular, median series; dorsal fin originating over or slightly anterior to the gill opening; pectoral fin present; posterior nostril a simple elliptical opening in front of mideye. For other characters, see the description below of *Boehlkenchelys longidentata,* the type species by original designation and monotypy.

Remarks.—*Boehlkenchelys* can be distinguished from most other chlopsid genera by the vomerine dentition. Only *Robinsia* and *Linkenchelys* have a single, median series of vomerine teeth. *Boehlkenchelys* can be distinguished from *Robinsia* by the presence of a pectoral fin. *Linkenchelys,* described by Smith (1989) as a chlopsid, also

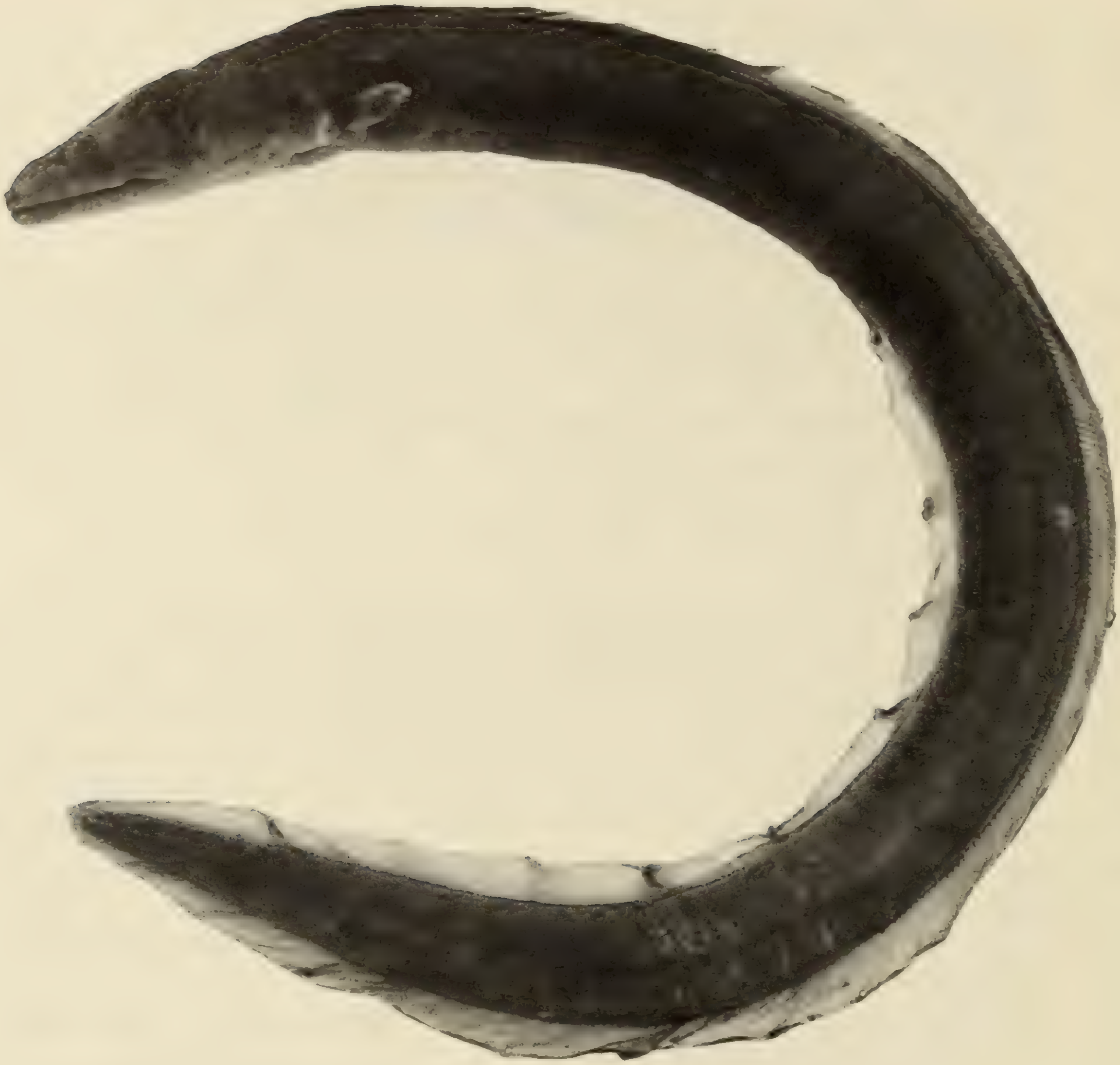

Fig. 1. Holotype of *Boehlkenchelys longidentata,* ROM 46990, 199 mm TL; North Astrolabe Reef, Fiji.

has a single, median series of vomerine teeth and a pectoral fin. It can be distinguished from *Boehlkenchelys* by its more posterior dorsal fin origin. Also, studies of additional specimens of *Linkenchelys* by the author and D. G. Smith have shown that this genus does not belong in the family Chlopsidae.

Etymology.—In recognition of their many contributions to the study of eels, the generic name is derived from the surname of Eugenia B. Böhlke and the late James E. Böhlke, and from *enchelys* (eel). The gender is feminine.

Boehlkenchelys longidentata, new species
Figs. 1–3

Kaupichthys nuchalis (not of Böhlke).—Winterbottom et al., 1989:6.

Holotype.—ROM 46990 (199 mm total length); Fiji, North Astrolabe Reef, on outer edge of reef on western side, 122–213 ft, 18°37′06″S, 178°30′21″E; A. R. Emery, R. Winterbottom, J. Payne and R. McKinnon; 24 Mar 1983.

Paratypes.—ROM 51964 (1, 132); same data as holotype. ROM 46989 (1, 162,

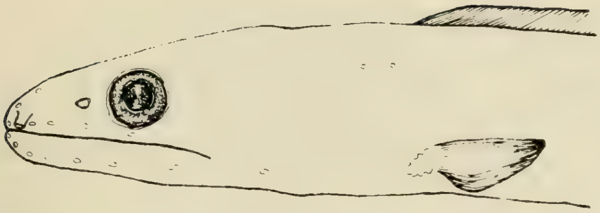

Fig. 2. *Boehlkenchelys longidentata,* ROM 46990, Holotype, 199 mm TL; head.

cleared and stained); Fiji, Usborne Pass to Astrolabe Reef, on the south part, on the outside of the reef, 20–23 m, 18°42′24″S, 178°30′15″E; A. R. Emery et al.; 21 Mar 1983. ROM 42505 (1, 61); Chagos Archipelago, Peros Banhos, Isle Fouquet, offshore reef, 40–43 m, 5°27′03″S, 71°48′57″E; A. R. Emery et al.; 8 Mar 1979. ROM 42506 (1, 201) and USNM 317168 (out of ROM 42506, 1, 145); Chagos Archipelago, Salomon Islands, between Isle Diabole and Isle Anglaise, 60–80 ft, 5°20′38″S, 72°12′38″E; R. Winterbottom et al.; 18 Mar 1979. BPBM 9420 (1, 114); Palau Islands, SW edge of Augulpelu Reef, 110–170 ft; J. E. Randall, A. R. Emery and E. S. Helfman; 22 Apr 1970. BPBM 19302 (1, 180); Molucca Islands, Ambon Island, point at NW side of village of Silale, SE side of Ambon Bay, 24–33 m; J. E. Randall and G. R. Allen; 25 Jan 1975. ANSP 163975 (1, 60); Fiji, Viti Levu, 100 yards S of E side of Mbengga Island, ca. 20 nautical miles SW of Suva Harbor, ca. 12–18 m; W. Smith-Vaniz et al.; 14 Apr 1974.

Diagnosis.—As for the genus.

Description.—Total vertebrae 125 (121–128), predorsal vertebrae 7 (6–8), preanal vertebrae 37 (34–37), precaudal vertebrae 95 (88–95). Dorsal-fin rays 363 (340–373), anal-fin rays 281 (253–294), pectoral-fin rays 16 (cleared and stained paratype). Proportions as percent of TL: predorsal length 12.6 (11.5–14.4), preanal length 37.2 (33.0–37.7), head length 13.1 (12.6–14.8), depth at anus 5.0 (4.6–7.6), pectoral-fin length 3.1 (2.8–3.8). Proportions as percent of head length: eye diameter 14.6 (12.2–16.2), interorbital width 15.4 (13.3–16.2), snout length 23.8 (21.5–24.5), tip of snout to rictus of jaw 46.9 (38.9–49.0), pectoral-fin length 23.8 (18.9–28.8).

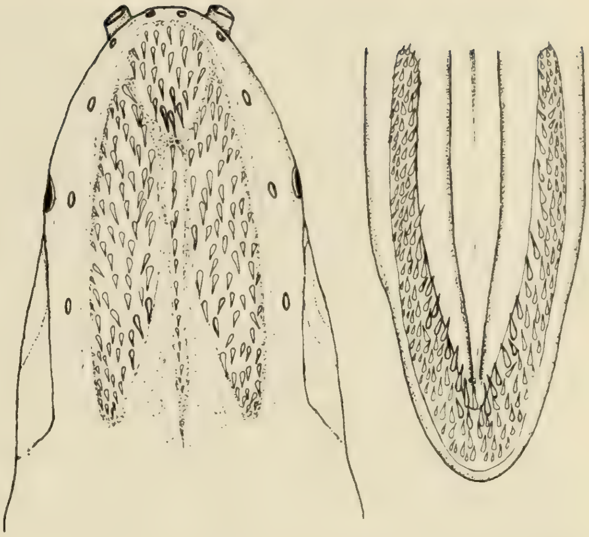

Fig. 3. *Boehlkenchelys longidentata,* ROM 46990, Holotype, 199 mm TL; dentition.

Body moderately elongate, slightly compressed. Dorsal fin begins above or slightly anterior to gill opening (Fig. 2). Pectoral fin well developed, rounded, almost twice eye diameter in length. Head moderate in length, relatively deep. Snout relatively deep, obtuse. Gape moderate, rictus behind posterior margin of eye. Anterior nostril tubular, slightly behind tip of snout, directed anterolaterally. Posterior nostril a simple elliptical opening in front of middle of eye.

Lateral line on body obsolete except for two (three in one paratype) pores in branchial region (Fig. 2). Supraorbital pores three: first (ethmoidal) at anteroventral tip of snout, second anteromedial to base of anterior nostril, and last above and behind anterior nostril. Infraorbital pores four: first just behind anterior nostril, second midway between anterior and posterior nostrils, third below posterior nostril, and last below middle of eye. Preoperculomandibular pores eight, seven before rictus and one behind.

Teeth long, slender, needle-like, depressible. Maxillary teeth (Fig. 3) in 6–7 irregular rows, increasing in size from outer to inner, a total of 14–18 teeth in the inner row. Mandibular teeth like those of the maxilla, except in 5–6 irregular rows with 18–24 teeth in the inner row. Vomerine dentition in a single, sometimes irregular row of 12–26 teeth.

Color of body uniform light olive-brown to brown; base of dorsal fin, caudal fin and posterior portion of anal fin darker. Colors in life similar (from color photograph of holotype).

Etymology.—The name *longidentata* is from the Latin *longus* and *dentatus,* in reference to the long, needle-like teeth.

Remarks.—One of the paratypes (ROM 42506, 201 mm TL) is a subadult to adult female with well developed ova 0.8–1.0 mm in diameter. This is probably close to the maximum size for this species.

Acknowledgments

I thank Richard Winterbottom for bringing the existence of this species to my attention, providing a portion of the type series, and allowing a paratype to be retained for the USNM collections. I also thank Eugenia B. Böhlke, John E. McCosker and David G. Smith for reviewing the manuscript, and Jennifer Westhoff for preparation of Fig. 3.

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JAMAICAN CRETACEOUS ECHINOIDEA (ECHINODERMATA). 3. *SCOLIECHINUS AXIOLOGUS* ARNOLD AND CLARK, 1927, AND AN INDETERMINATE CASSIDULOID

Stephen K. Donovan

Abstract.—Two rare echinoids from the Late Cretaceous of Jamaica are described. *Scoliechinus axiologus* Arnold & Clark, 1927, is the earliest known toxopneustid and is distinguished on the basis of its unusual ambulacral plating. The Cretaceous age of this species is confirmed. A unique but incomplete test of a large cassiduloid represents a taxon new to the Antillean region and is possibly a member of the family Faujasiidae.

The only diverse echinoid faunas of Cretaceous age that have been described from the Antillean islands come from Jamaica and Cuba. Species from Jamaica were mainly described in a brief series of papers in the 1920s (Hawkins 1923, 1924; Arnold & Clark 1927). With the exception of the cidaroids (Cutress 1980), the Jamaican fauna has subsequently been largely ignored. Multiple specimens are now available for many species, most of which were originally described from one or two tests only, and new species have been discovered. The present paper forms part of a series of contributions in which the entire Cretaceous echinoid fauna of Jamaica is to be reinvestigated on the basis of these improved collections.

Specimens described herein are deposited in the collections of the Museum of Comparative Zoology at Harvard (MCZ) and the Natural History Museum, London (BMNH). Descriptive terminology follows Melville and Durham (1966) and Smith (1988). The terminology of open nomenclature relies on the criteria advocated by Bengtson (1988).

Class Echinoidea Leske
Order Echinoida Claus
Family Toxopneustidae Troschel

Remarks.—The toxopneustids have previously been placed within the order Temnopleuroidea (see, for example, Fell & Pawson 1966:U426), but were reclassified as members of the order Echinoida by Smith (1984:171).

Genus *Scoliechinus* Arnold & Clark

Type species.—*Scoliechinus axiologus* Arnold & Clark, 1927, by original designation.

Other species.—None.

Diagnosis.—Small, hemispherical test with moderately broad ambulacra. Pore pairs in triads, showing trigeminous echinoid compounding of distinctive pattern (Fig. 2D), with pores of middle component outermost. Adapically, interambulacra are mainly naked interradially. Peristome large, rounded, with elongate buccal notches.

Scoliechinus axiologus
Arnold & Clark, 1927
Figs. 1, 2

Scoliechinus axiologus Arnold & Clark, 1927:23–24, pl. 2, figs. 7, 8; 1934:140.—Mortensen, 1943:465–466, fig. 292a–c.—Fell & Pawson, 1966:U429, fig. 320.2.—Kier & Lawson, 1978:44.—Donovan, 1988:table 1; 1992a.—Donovan & Bowen, 1989:59, text-figs. 2, 3.

Material, locality and horizon.—Holo-

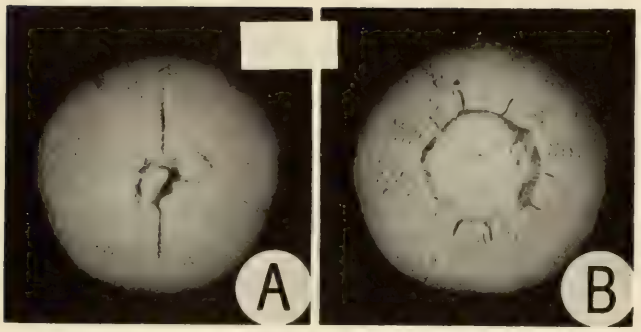

Fig. 1. *Scoliechinus axiologus* Arnold & Clark, 1927, holotype, MCZ 3268. A, Apical view; B, Oral view. Scale bar represents 10 mm.

type, MCZ 3268 (Fig. 1), plus a second (non-paratype) specimen, MCZ 3498. The type locality is in the "Leyden region, St. James Parish" (Arnold & Clark 1927:23). Previous authorities have suggested the age to be Cretaceous (Donovan 1988, Donovan & Bowen 1989), questionably Cretaceous (Mortensen 1943, Fell & Pawson 1966), or even Eocene (Kier & Lawson 1978). Leyden is within the outcrop area of the Cretaceous rocks of the Sunderland Inlier (Donovan & Bowen 1989:fig. 1H) and *S. axiologus* probably comes from the Newmans Hall and Sunderland Shales, of Late Campanian age (Green undated). The only other echinoids recorded from this inlier are spatangoids (Chubb 1958:8), probaly *Hemiaster.* The locality of MCZ 3498 is unknown (Arnold & Clark 1934:140).

Preservation.—The holotype is slightly crushed, with cracks radiating from the apex along sutures between plate columns. The apical region of the corona is irregular in shape due to crushing (Fig. 2A). The second specimen is water-worn, with some regions of the test cracked or broken away, probably due to post-exhumation abrasion.

Diagnosis.—As for the genus.

Description.—Test hemispherical, rounded pentagonal to circular in outline. Ambitus low, at about 25% of the height of the test. Test gently domed adapically, flattened adorally. Peristomal margin slightly depressed.

Apical disc not preserved (apart from an indistinguishable fragment on MCZ 3498), but much smaller than the peristome and polygonal in outline (Figs. 1A, 2A).

Ambulacra wide, about 26% of the test diameter at the ambitus in the holotype, and straight. Pore pairs arranged in triads, with plates showing trigeminous echinoid compounding (compare Fig. 2C, D with Smith 1984:fig. 3.6). Pores of middle component outermost (Fell & Pawson 1966:U429). Primary ambulacral tubercles smooth, imperforate and non-crenulate, about as large as interambulacral secondary tubercles. Secondary tubercles of poriferous zones slightly smaller than primaries; small tertiary tubercles also present. Adapically ambulacra mainly naked perradially, although flanked by tubercles. Perradial tubercles become abundant about 50% of height of test below the apex and are present to margin of peristome (Fig. 2B). Ambulacra widest at ambitus, where interporiferous zone is as wide as combined widths of poriferous zones. Interporiferous zone tapers to peristome.

Adapically interambulacra mainly naked interradially, bordered by densely packed tubercles. Tubercles only occur interradially from just adapically of ambitus to margin of peristome. Four sizes of interambulacral tubercle apparent, all smooth, imperforate and non-crenulate. Primary tubercles offset in double columns adradially. Large tubercles most densely packed adorally.

Persitome large, central, rounded pentagonal in outline and depressed. Elongate buccal notches present (Fig. 2B).

Measurements.—See Table 1.

Remarks.—*Scoliechinus axiologus* is the rarest of the regular echinoids so far described from the Jamaican Cretaceous, being known from only one inlier and two specimens. The only other regular echinoids of this age known from only one locality on the island are two species of cidaroids (Donovan 1992a:fig. 3) described from radioles only (Cutress 1980). Other taxa described from tests have been collected from two or more localities; some of these species are also known from Cuba.

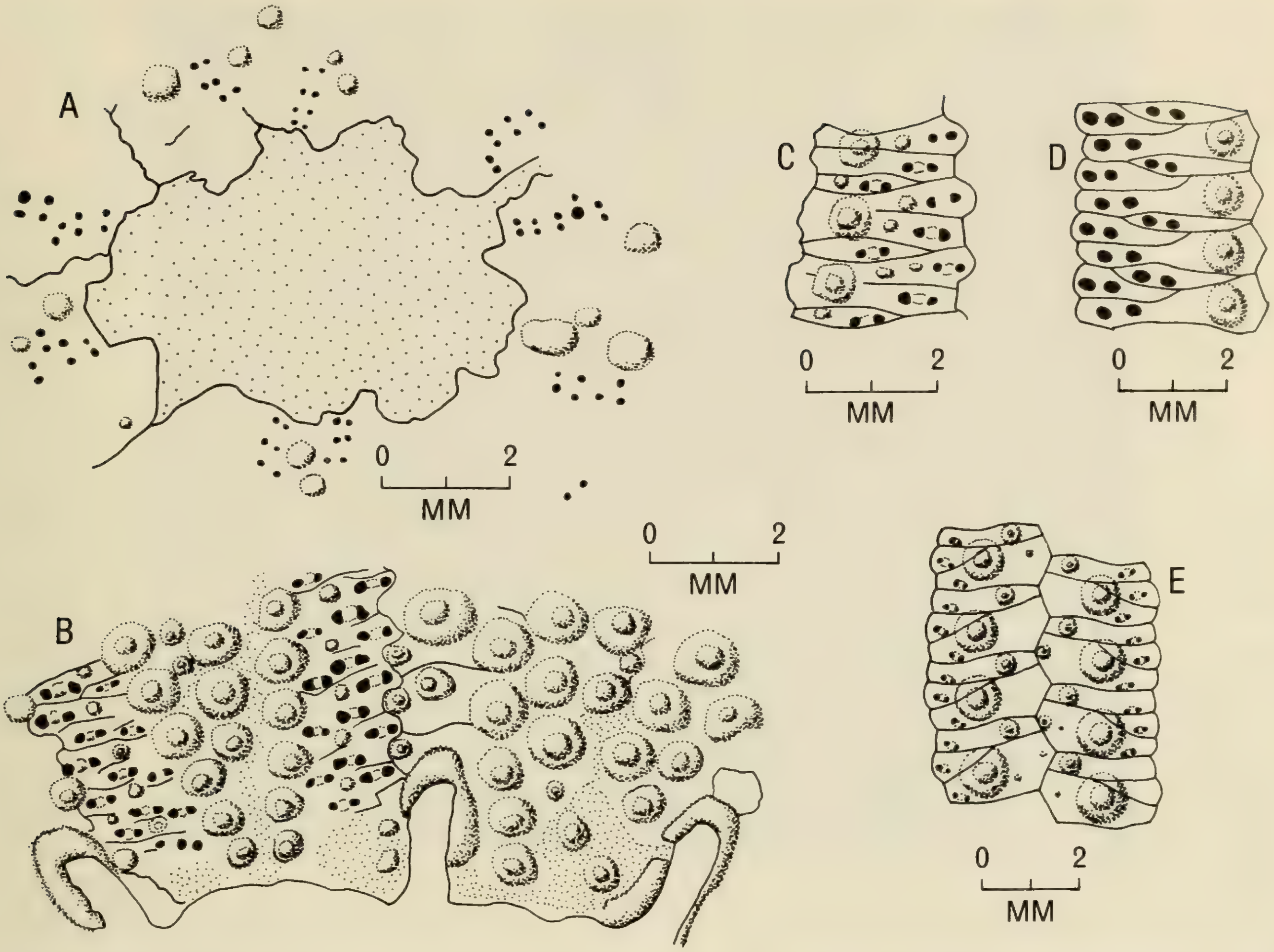

Fig. 2. A–D, *Scoliechinus axiologus* Arnold & Clark, 1927: A–C, holotype, MCZ 3268. A, Outline of (missing) apical system; B, Detail of test adjacent to peristome; C, Detail of part of an ambulacral column; D, MCZ 3498, detail of part of an ambulacral column (redrawn after Mortensen 1943:fig. 292c); E, Detail of part of an ambulacrum of *Lytechinus euerces* H. L. Clark (redrawn after Fell & Pawson 1966:fig. 321.2). A–C are camera lucida drawings.

In his analyses of echinoid phylogeny, Smith (1981:text-fig. 7; 1984:fig. A.1) indicated that valid toxopneustid fossils range back to the Miocene, although the presumed origin of the group was in the Late Cretaceous. *S. axiologus* thus appears to be the earliest known toxopneustid. The unusual pattern of trigeminous echinoid plate compounding shown by the ambulacra, now shown to occur in both specimens (Fig. 2C, D), is comparable to that of *Lytechinus* (Fell & Pawson 1966:U429; Fig. 2E). Some confusion has existed concerning the precise pattern of ambulacral plating in this species, which Arnold & Clark (1927:23) described (but unfortunately did not figure) thus: "... pore-pairs in arcs of three but these arcs are most evident when test inverted; in normal position, the inner, upper pore-pair is so considerably separated from the other two by a pair of large secondary tubercles it does not seem to belong to them but rather with the two pairs of the next plate above, especially since the pore-pair of the next element below lies far outside the natural curve of the arc; ambulacral plates echinoid, consisting of three elements of which the adoral, a well-marked primary, is largest; middle element usually a primary, though apparently it does not always reach the midline [see below]; aboral element clearly a demiplate, not reaching outer margin of ambulacrum; median element projects conspicuously into interambulacral area, beyond basal element." Mortensen (1943:465) considered that this description of the am-

Table 1.—Measurements taken from the two known specimens of *Scoliechinus axiologus* Arnold & Clark, 1927. Key: * = holotype slightly crushed, particularly at the apex.

	MCZ 3268	MCZ 3498
Test diameter, mm	25.0–25.5	26.2–26.9
Test height, mm	ca. 14.0	ca. 16.0
Apical disk diameter, mm	4.2–6.2*	4.4–4.8
Interambulacrum width at ambitus, mm	9.1	ca. 9.6
Ambulacral width at ambitus, mm	ca. 6.5	6.8
Interambulacral plates per column	ca. 22	23
Ambulacral pore pairs per column	ca. 84	?
Ambulacral primary tubercles per column	ca. 28–29	?
Height of ambital interambulacral plate, mm	ca. 1.2	1.2
Width of ambital interambulacral plate, mm	ca. 4.5	ca. 4.8
Peristome diameter, mm	10.5–11.0	ca. 11.5

bulacral structure "... is not easily understood ..." and borrowed MCZ 3498 (that is, not the holotype) to illustrate this structure (Mortensen 1943:fig. 292c; Fig. 2D herein). For comparison, part of the ambulacral plating of the holotype is illustrated herein (Fig. 2C). Whereas the figured patterns of plating differ in detail, the plating of the holotype does appear to approach that of MCZ 3498 in some places, a variation that Arnold & Clark seem to have recognized (see above). However, MCZ 3498 is water-worn and the plate boundaries are much more readily apparent than in the holotype, and it may be that Fig. 2C is, in fact, incorrect due to the problems of identifying plate sutures on a better preserved test. It is therefore suggested that Mortensen's diagram (Fig. 2D) should be considered to be the more accurate of the two interpretations illustrated herein until more specimens become available and the range of morphology shown by the ambulacral plating in this species can be fully analyzed.

Order Cassiduloida Claus
Family Faujasiidae? Lambert
Cassiduloid sp. indet.
Figs. 3–5

Cassiduloid sp.—Donovan & Bowen, 1989: 60, text-figs. 2, 3.

Cassiduloid sp. indet.—Donovan, 1992a.

Material, locality and horizon.—A unique specimen, BMNH E83009 (Fig. 3), from the Guinea Corn Formation (Late Campanian to mid Maastrichtian; Jiang & Robinson 1987) of the Central Inlier of Jamaica (Donovan & Bowen 1989:text-fig. 1Q). Dr. A. G. Coates (in litt.) has identified the label 'CG12' on the specimen as indicating a Geological Survey Division, Jamaica, locality in the type section of the Guinea Corn Formation in the Rio Minho bed, downstream from the confluence with the Rock River and from within the top 6 m of the Formation (approximate grid reference 416456). This part of the succession approximates locality 3 of Robinson (1988), which has also yielded ?*Pygopistes rudistarum* (Hawkins, 1923; see Donovan & Bowen 1989) and *Goniopygus supremus* Hawkins, 1924 (see Donovan 1990). From its occurrence high within the Guinea Corn Formation, the new cassiduloid is undoubtedly Maastrichtian in age.

Preservation.—The specimen is cemented in a well-indurated block of limestone, with only the apical (Figs. 3, 4) and part of the lateral (Fig. 5A) surfaces exposed. The test is fractured (Figs. 3, 4) across and along plate sutures (as seen in some ambulacra). Some obvious 'thrusting' of plates has occurred, such as in interambulacrum 2, which has been forced over ambulacrum II (Figs. 3, 4).

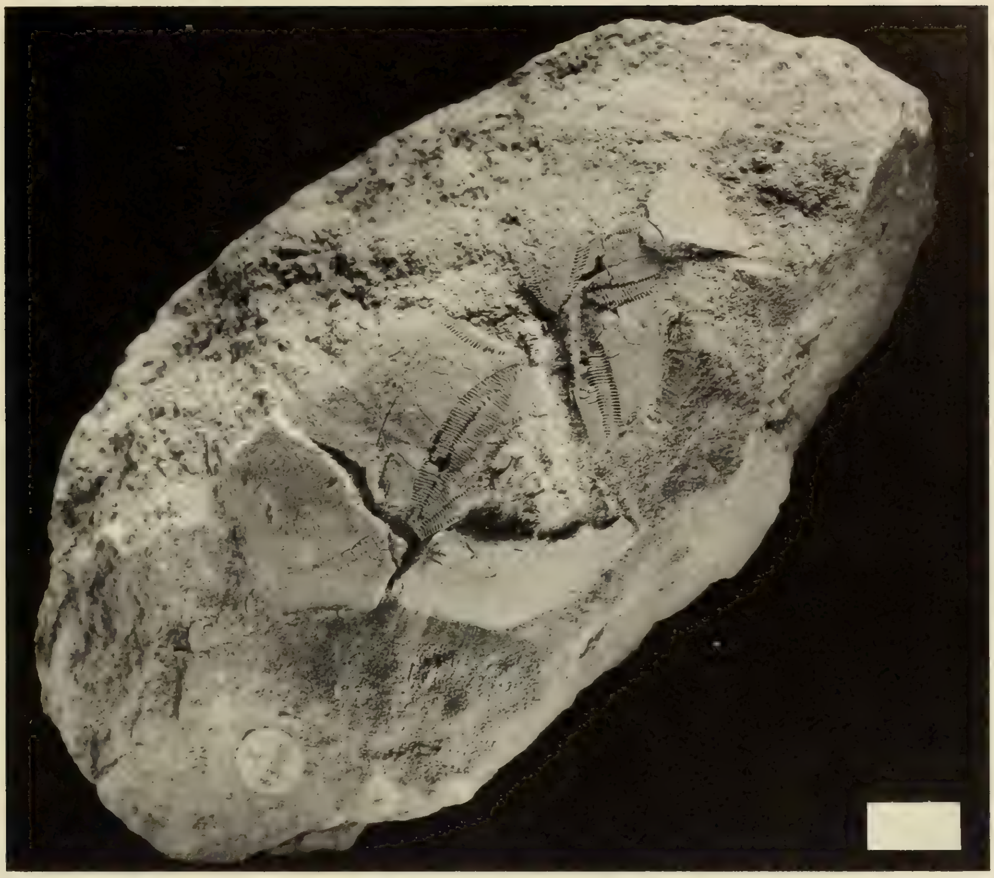

Fig. 3. Cassiduloid sp. indet., BMNH E83009, apical view. Scale bar represents 10 mm.

The test was water-worn prior to collection. This has removed much of the tuberculation, except around the exposed margins of the specimen, adjacent to the sediment surface. However, the corollary of this process has been to emphasize the positions of the plate boundaries (Fig. 4) and fine details, such as the conjugate anisopores of the ambulacral petals, are well-exposed (Fig. 5B).

Description.—Test at least moderately high (at least 30 mm; Fig. 5A), and longer than wide (Figs. 3, 4). Visible part of test obviously incomplete, but about 50 mm in length. A fragment of madreporite is preserved (Fig. 4, arrow).

At least part of the plating of each ambulacrum is apparent. Ambulacra petaloid adapically and flush with test surface, widening adorally of petals. Petals closed, with conjugate anisopores (compare Fig. 5B with Smith 1980:pl. 3, figs. 2–4) immediately adjacent to the adoral suture of each plate. Interporiferous zones broad. Petal V (Fig. 4) best preserved, approximately 23 mm long with a maximum width of 10 mm. Ambulacral plates of petals low and numerous. Plates higher adorally, with isoporous pore pairs.

Interambulacra (except 3) partially preserved adapically. Interambulacral plates arcuate, increasing in height and rapidly increasing in width away from apical system. Tubercles, where preserved, closely-spaced, slightly depressed, of equal size, and perforate.

Peristome and periproct not visible.

Remarks.—The breakage of echinoid tests across plate sutures is normally associated with damage sustained while the organism was alive (Smith 1984:19, fig. 2.6f), either by predation or fragmentation in a turbulent environment. However, it is improbable that either of these would have left the various fragments of the test in such close association. It is more likely that this specimen was

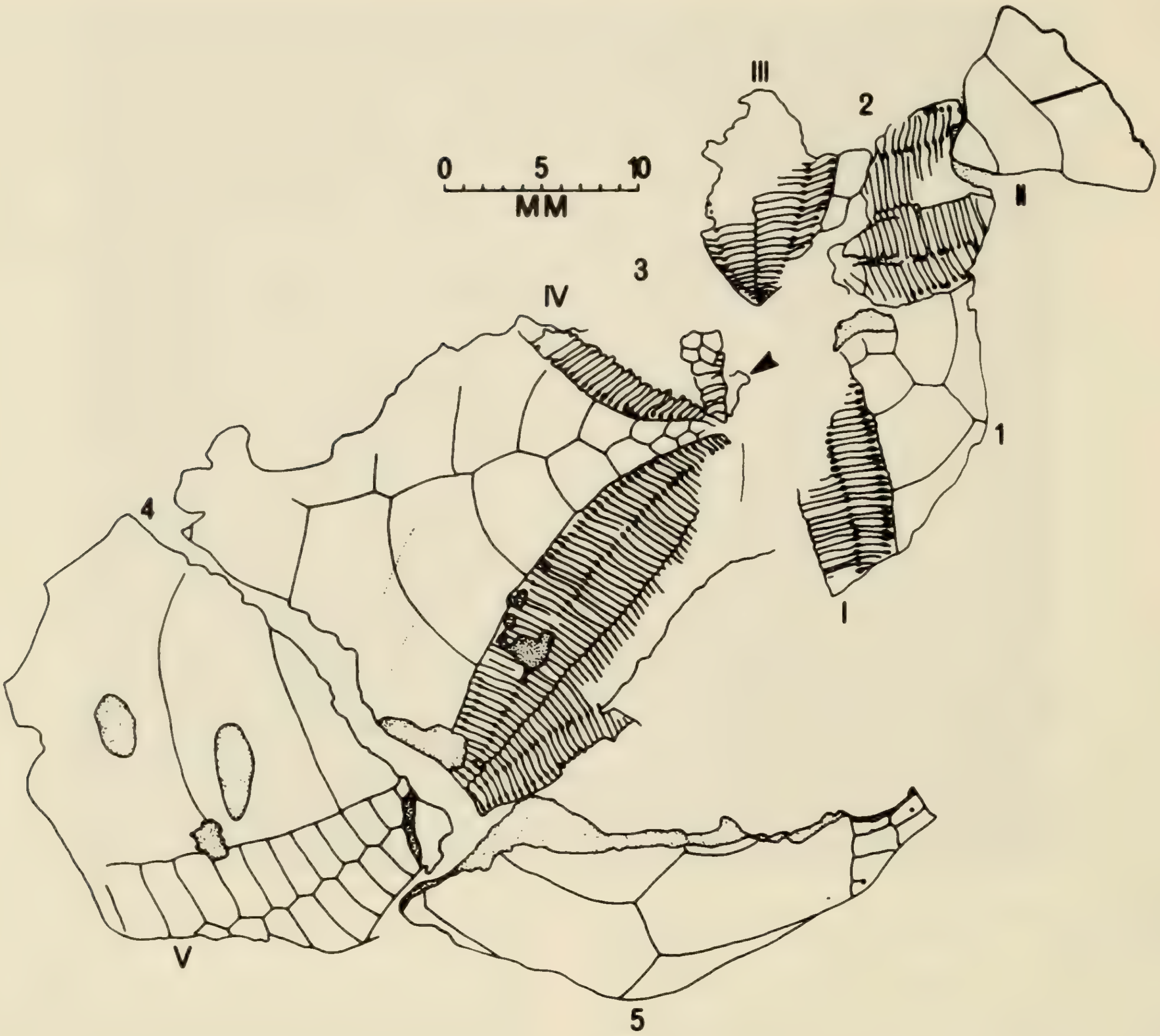

Fig. 4. Cassiduloid sp. indet., BMNH E83009, apical view, camera lucida drawing. Ambulacra (I–V) and interambulacra (1–5) are indicated. Broken plate surfaces are stippled. The madreporite is arrowed.

broken during transport, perhaps entombed within a bioclastic turbidity flow over a short distance, producing extensive breakage, but keeping the fragments of the test in close association. Kidwell & Baumiller (1990) have demonstrated that fragmentation during transport of regular echinoid tests occurs much more readily after a period of soft tissue decay (which removes the mutable collagenous tissues which hold the coronal plates in close association) than when 'fresh.' However, transport in a fluidized sediment body may have been more destructive than the experimental tumbling without grit, preventing speculation on whether this specimen was buried alive or was recently dead. As it is a cassiduloid, it may well have been preserved infaunally for some time following death and following transport. There is no evidence of post-mortem encrustation by epibionts. Moreover, interlocking stereom trabeculae between ossicles (cf. Donovan 1991:fig. 11.2C) may have strengthened the test and held the coronal plates in close association, even after the decay of the mutable collagenous tissues. It is uncertain whether this pattern of breakage could be produced by compaction alone (Rettger 1935).

The interpretation and numbering of the Carpenter rays in this specimen (Fig. 4) is slightly subjective, but is in all probability correct. The two most elongate petals are adjacent and these have been interpreted as the paired posterior petals, V and I. Evidence from petals consequently interpreted as anterior suggests that they were relatively broader (see, in particular, II and IV in Fig.

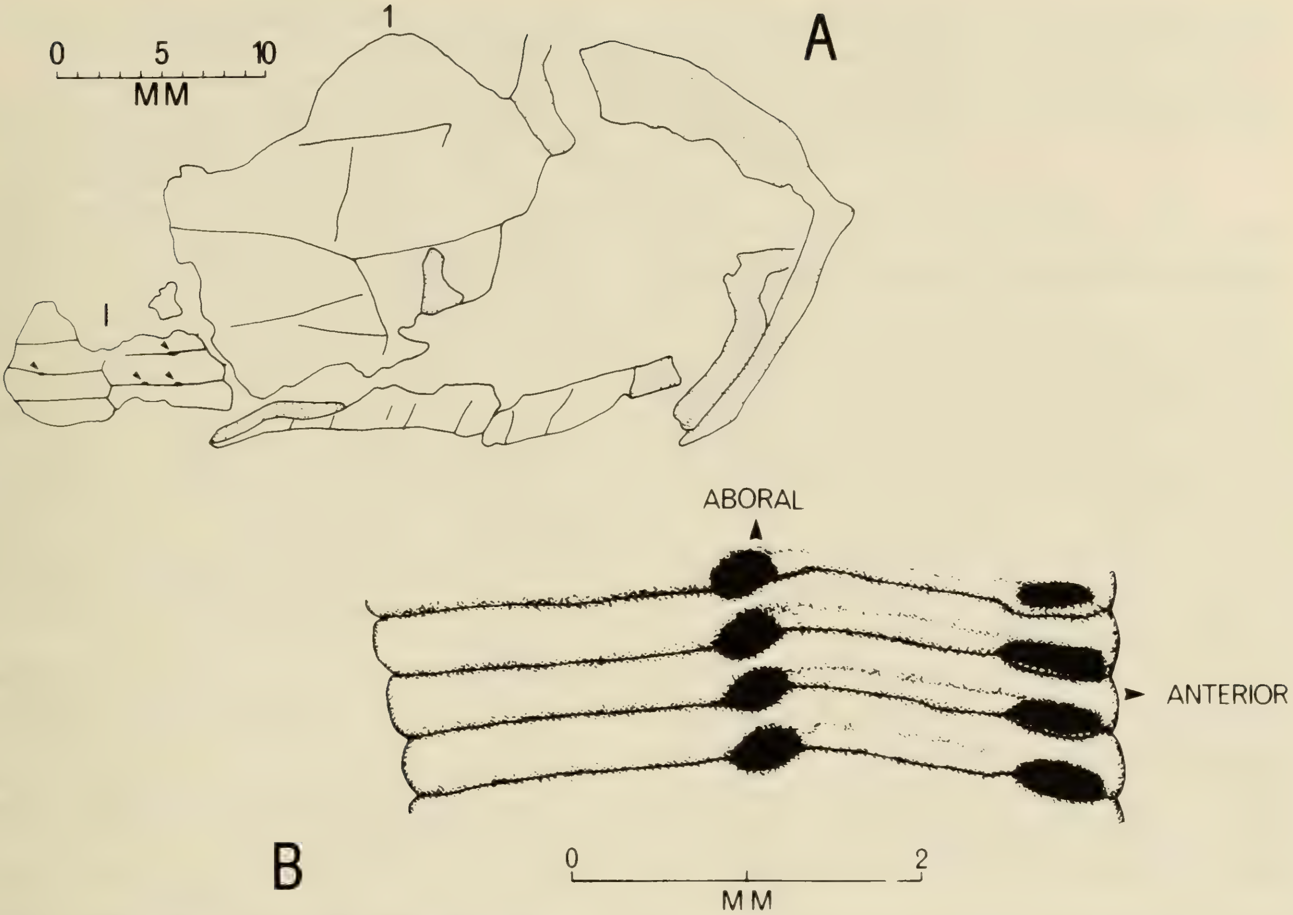

Fig. 5. Cassiduloid sp. indet., BMNH E83009, camera lucida drawings. A, Lateral view of test, showing ambulacrum I and interambulacrum 1. Arrows indicate ambulacral pores. Broken plate surfaces are stippled. B, Conjugate anisopores in the petal of ambulacrum I.

4). The petaloid ambulacra show that this specimen is not a holectypoid (Kier 1962: 22) and by the Maastrichtian no spatangoid had an anterior petal (Dr. A. B. Smith, pers. comm.).

This specimen is very different from other irregular echinoids known from the Cretaceous of Jamaica, although two other species of cassiduloids have been reported from this interval. ?*Pygopistes rudistarum* (Hawkins, 1923; see Donovan & Bowen 1989) has open petals, with pore pairs relatively more closely spaced within petals. An undescribed nucleolitid sensu lato (Donovan, research in progress) has the periproct situated in a prominent posterior groove on the aboral surface. Of the other irregular echinoids from the Jamaican Cretaceous, *Metholectypus trechmanni* Hawkins, 1923, lacks petals, while *Hemiaster* sp. or spp. has four short petals which occur in weak to strong depressions (Donovan 1992a:figs. 10, 13, respectively). It is also relevant to note that cassiduloid sp. indet. is larger than any of the known specimens of these other species and is not morphologically similar to any of the Jamaican Cenozoic cassiduloids (Donovan 1992b) or with any Cretaceous echinoids from Cuba (Sánchez Roig 1949).

Dr. A. B. Smith (pers. comm.) has suggested that the Guinea Corn cassiduloid most closely approaches the family Faujasiidae Lambert. The following features taken from the diagnosis of the family by Kier (1966:U508) can be compared with the Jamaican test: "Small to large, commonly broad . . . petals equal, broad, closed . . . outer pore slitlike; single pore in all ambulacral plates beyond petals. . . ." The Jamaican specimen agrees well with all of these criteria, although a single ambulacral plate adoral of the petals does appear to possess a pore pair (Fig. 5A). This may be an artifact, as other plates are single-pored. A closer comparison will require superior material.

Acknowledgments

My interpretation of the cassiduloid sp. indet. was greatly improved and corrected following constructive reviews by Andrew Smith and David Lewis (both BMNH). David Lewis also arranged for this specimen to be photographed. I also thank Tony Coates (George Washington University) for his comments on the locality of cassiduloid sp. indet. Loan of MCZ specimens of *S. axiologus* was kindly arranged by Felicita d'Escrivan. The holotype was photographed by the author, using equipment kindly made available by David Pawson, during the period of a Smithsonian Institution Short Term Visitors Grant at the National Museum of Natural History in 1989, which I gratefully acknowledge.

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THE FLAT BUG GENUS *CALISIOPSIS* CHAMPION: A REVIEW WITH DESCRIPTIONS OF THREE NEW SPECIES, INCLUDING ONE FROM DOMINICAN REPUBLIC AMBER (HETEROPTERA: ARADIDAE)

Richard C. Froeschner

Abstract.—A review of the Neotropical flat bug genus *Calisiopsis* Champion gives a key to separate its nymphs from those of *Calisius* Stål; a diagnosis, habitus drawing, and lectotype designation for the type-species *C. ampliceps* Champion; descriptions and habitus drawings of three new species [*C. brodzinskyorum* found in amber from the Dominican Republic, *C. kormilevi* from a forest canopy in Peru, and *C. nigrotuberculata* from Mexico]; and a key to the seven known species.

Discovery of three new species of *Calisiopsis* Champion, one represented by a single specimen in amber from the Dominican Republic, one consisting of a series of adults and nymphs taken during a survey of a forest canopy in Peru, and the third a single specimen from Mexico, presented an opportunity to review the genus and offer a key to its seven species.

The existence of an amber fossil hemipteran of a modern genus not otherwise represented on Hispaniola is not unique here; Popov (1987a, 1987b) described amber specimens in two modern genera of assassin bugs (Reduviidae: *Malacopus* Stål and *Empicoris* Wolff) not previously cataloged from this large island.

Fortunately, the primary types of all of the previously described species were available for examination: the syntypes of the type-species lent by The Natural History Museum in London; the other three in the Smithsonian Institution, National Museum of Natural History. All measurements given below are in millimeters.

Genus *Calisiopsis* Champion

Calisiopsis Champion, 1898:67. Type species: *Calisiopsis ampliceps* Champion, only included species.

Champion's genus *Calisiopsis* was treated as a junior synonym of *Calisius* Stål (1860: 68) by Usinger and Matsuda (1959:93), but in that latter year it was diagnosed as a distinct genus by Kormilev (1959a:210; see also 1959b:320) who presented the following couplet to separate the two genera:

Anterior process of the head more robust; antennae normal, generally with the segments increasing in length from the first to the fourth; hypopygium of the male big, dorsocaudal or caudal in position, clearly visible from above . . . . *Calisius*

Anterior process of the head relatively narrower and more protruding; the first three antennal segments very short, moniliform, the fourth as long, or almost as long, as the first three together, and granulated; hypopygium of the male flat, displaced on the ventral surface, and removed from the hind border, not visible from above . . . *Calisiopsis*

Later, when presenting a key to the six genera of the subfamily Calisiinae Stål, Kormilev (1986:249–250) again recognized that the elongate and dotted antennal segment IV separated *Calisiopsis* from *Calisius* in which the undotted antennal segment IV was shorter than the combined lengths of antennals I–III. Four species of *Calisiopsis* were keyed by Kormilev (1976:70) and cataloged by Kormilev and Froeschner (1987: 57–58).

Apparently the nymphs of *Calisiopsis* have not yet been characterized. Fortunately, the series of the new species *C. kormilevi* included a number of nymphs of several instars; a dorsal habitus drawing of a fifth-instar nymph is herein given as Fig. 5. In all of these nymphs, plus an unidentified *Calisiopsis* nymph from Mexico, the very short antennal segments I–III combined were about as long as or very slightly shorter than the large, fusiform, antennal segment IV. On these nymphs the location of each scent gland opening at the apical margin of abdominal segments III–V plus the pattern of the glabrous areas confirm Usinger and Matsuda's (1959:93) conclusion that the subfamily Calisiinae is more similar to the subfamily Aradinae than to the subfamily Mezirinae [see their figs. 12a and 12c] to which it was once assigned. Comparing this pattern with the only fifth-instar nymph of the genus *Calisius* (*C. homalantha* Kormilev) at hand permits making the following couplet to separate the last nymphal instars of these two genera [recognizing the fact that material is available for only one species in each genus]:

Antennal segment IV with numerous small pale dots, its length as long as or longer than combined lengths of moniliform segments I–III. Median scent gland openings prominent, surrounded by darkened ring. Entire series of inner glabrous areas subequal in size, broader than transverse width of scent gland opening. Glabrous areas of second row from midline smaller than the inner series, becoming progressively smaller posteriorly. Fig. 5 .... *Calisiopsis*

Antennal segment IV not dotted, its length distinctly shorter than combined lengths of cylindrical segments I–III. Median scent gland openings smaller than in *Calisiopsis*, edges concolorous with surrounding dorsum. Both rows of glabrous areas inconspicuous, much smaller than gland openings .... *Calisius*

Key to adults of the species of *Calisiopsis*

1. Scutellar disc between median carina and lateral margins with evident elevated blunt tubercles 2
– Scutellar disc without elevated tubercles 4
2. Head, in lateral view, with dorsal outline of anterior lobe directed approximately at midheight of eye (Fig. 7). Interocular area of head, including midline, distinctly lower than dorsal margin of eye. Length 2.8–3.4. (Figs. 2, 7) .... *kormilevi*
– Head, in lateral view, with dorsal outline of anterior lobe directed much above midheight of eye. Interocular midline as high as dorsal margin of eye 3
3. Tubercles on anterior lobe of head short, blunt, arranged in two rather regular, well separated, longitudinal rows: 1 lateral, 1 dorsolateral. Tubercles along free edge of connexivum, except one at posterior angle of each segment, inconspicuously small. Length 3.4 (Fig. 3) .... *nigrotuberculata*
– Tubercles on anterior lobe of head, especially anteriorly, longer than wide, irregularly placed. Tubercles along free edge of connexivum all prominently projecting. Length 3.4 (Fig. 4) .... *brodzinskyorum*
4. Head with anterior lobe outlined laterally by a single row of large, prominently radiating, blunt tubercles. Length 3.6 (Fig. 6) .... *planiceps*
– Head with anterior lobe laterally with scattered small tubercles or none 5
5. Tubercles on midline of interocular area, viewed anteriorly, slightly

higher than dorsal margins of eyes. In lateral view, anterior lobe of head with dorsal outline directed at or slightly above dorsal margin of eye. Length 2.9 (Fig. 8) .... *minuta*

– Tubercles on midline of interocular area, viewed anteriorly, distinctly lower than dorsal margins of eyes. In lateral view, anterior lobe of head with dorsal outline directed well below dorsal outline of eye 6

6. Anterior lobe of head, in lateral view, with dorsal outline subhorizontal, directed slightly below midheight of eye. Length 3.0 .... *brasiliensis*

– Anterior lobe of head with dorsal outline clearly diagonal, directed toward upper fourth of eye. Length 2.8–2.9 (Fig. 1) .... *ampliceps*

Calisiopsis ampliceps Champion
Fig. 1

Calisiopsis ampliceps Champion, 1898:67 (new species: Panama).

Diagnosis.—This species differs from all other known species in the genus by the combination of the lack of elevated tubercles on each side of the scutellar median carina plus the dorsal outline of the anterior head lobe being directed at the upper fourth of the eye.

This species appears to be known only from the type series, which consisted of three Panamanian specimens: two from Bugaba and one from Tolé. Champion commented that the Tolé specimen showed some differences and added "it may belong to a different species"—thus actually excluding it from the cotype series.

Through the kind cooperation of W. R. Dolling of the British Museum (Natural History), London, and T. J. Henry of the U.S.D.A., Systematic Entomology Laboratory, I was able to examine the two Bugaba specimens. They are glued side-by-side on a pinned cardboard rectangle—the left one, a male, ventral side up, the right one, a female, dorsal side up. The two specimens undoubtedly represent the same species and I hereby designate the right specimen (dorsal side up) as the lectotype. The six labels read, (1) "♀"; (2) "Type" [a red-bordered circular label, apparently labeled subsequent to Champion's study]; (3) "B.C.A. Rhyn.II. *Calisiopsis ampliceps* Ch.♀"; (4) "Bugaba, Panama, Champion;" (5) "Sp. figured"; (6) "Lectotype designation by Froeschner, 1991-right spm."

The various subsequent descriptive treatments of *C. ampliceps* were based on misdeterminations. Kormilev (1959a:222) recognized his earlier (1956:149) error based on a Brazilian specimen and made that specimen the holotype of his new species *Calisiopsis brasiliensis.* However, the specimen which he treated as *C. ampliceps* in his 1959a paper is not the same as Champion's species; it is here described as the new species *Calisiopsis nigrotuberculata.*

Distribution.—Panama.

Calisiopsis brasiliensis Kormilev

Calisiopsis ampliceps.—Kormilev, 1956: 149.

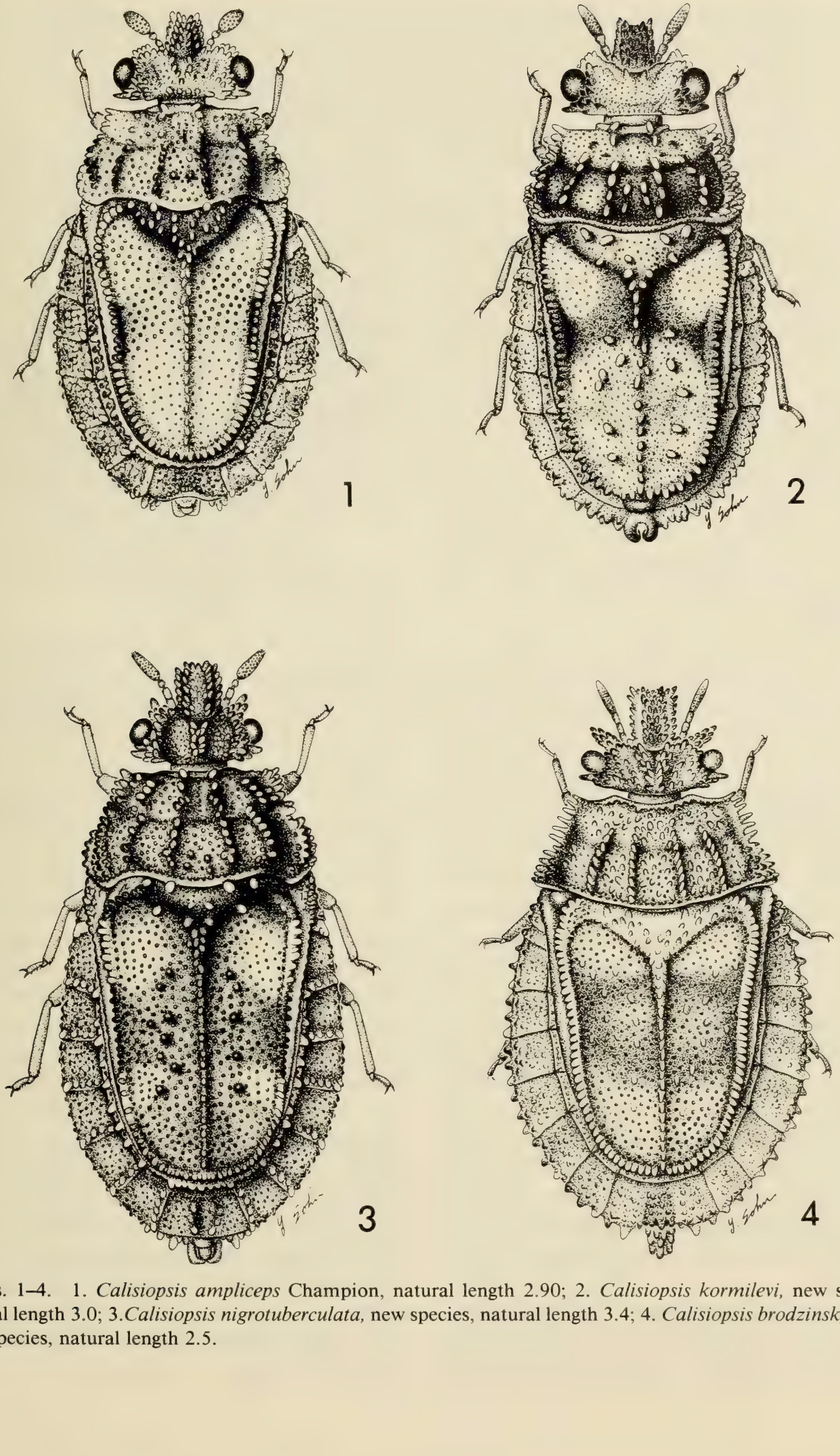
Calisiopsis brasiliensis Kormilev, 1959a:222 [new species: Brazil].

Diagnosis.—This species may be distinguished from all other known members of the genus by the combination of lack of elevated tubercles each side of the median scutellar carina plus the dorsal outline of the anterior head lobe directed slightly below the midheight of the eye. Because the head is missing from the holotype (the only known specimen), the head character used in the above key was derived from statement in the original proposal.

Distribution.—Brazil.

Calisiopsis brodzinskyorum, new species
Fig. 4

Diagnosis.—As keyed above, this fossil species may be recognized among the known



Figs. 1–4. 1. *Calisiopsis ampliceps* Champion, natural length 2.90; 2. *Calisiopsis kormilevi,* new species, natural length 3.0; 3.*Calisiopsis nigrotuberculata,* new species, natural length 3.4; 4. *Calisiopsis brodzinskyorum,* new species, natural length 2.5.

species of the genus by the combination of the scutellum having weakly elevated pale tubercles on each side of the scutellar midline, the interocular area of the head not depressed, and the tubercles along the free edge of the connexivum prominently projecting.

Description.—Holotype ovate, length 2.50, greatest width 1.28. Aspect typical for genus with tubercles on head, in 4 longitudinal rows on pronotum, and along margins of pronotum, abdomen, and scutellum.

Head: Wider than long, 0.71:0.49; anterior lobe with numerous scattered tubercles laterally and dorsolaterally, dorsal outline pointing to upper margin of eye. Antenna about two-thirds as long as head, segments I–III very short, almost moniliform (awkwardly positioned in the amber, making accurate measuring impossible), their combined lengths as long as IV, latter with small pale dots.

Pronotum: Wider than long, 1.24:0.49; anterior margin sinuately transverse, collar not projecting; posterior margin slightly convex. Scutellum with mediobasal triangular elevation bearing a few tubercles, midline behind it marked by a row of low tubercles; disc each side of midline with a few tubercles scattered, not in rows. Connexival segments and their laterotergites appearing flat, without an elevated rim between them.

Abdomen ventrally without tubercles.

Color: Mostly brown (appearing translucent in the amber), base and apical third of scutellum noticeably paler; tubercles apparently concolorous with surrounding exoskeleton. Legs dark, apparently without pale markings.

Holotype ♀.—Dominican Republic, in amber. The species description is based on a lone specimen in the Brodzinsky/Lopez-Penha collection now in the National Museum of Natural History, Smithsonian Institution.

Comments.—In Davis' (1989:545–550) discussion of that collection of amber, he noted that the amber "is found as secondary deposits in mid-Tertiary sandstone marine silts which may range between 20–30 million years in age"; because the amber was covered by the particles forming the sandstone it must be older than the stone. As yet, no modern species of *Calisiopsis* has been reported from the Dominican Republic.

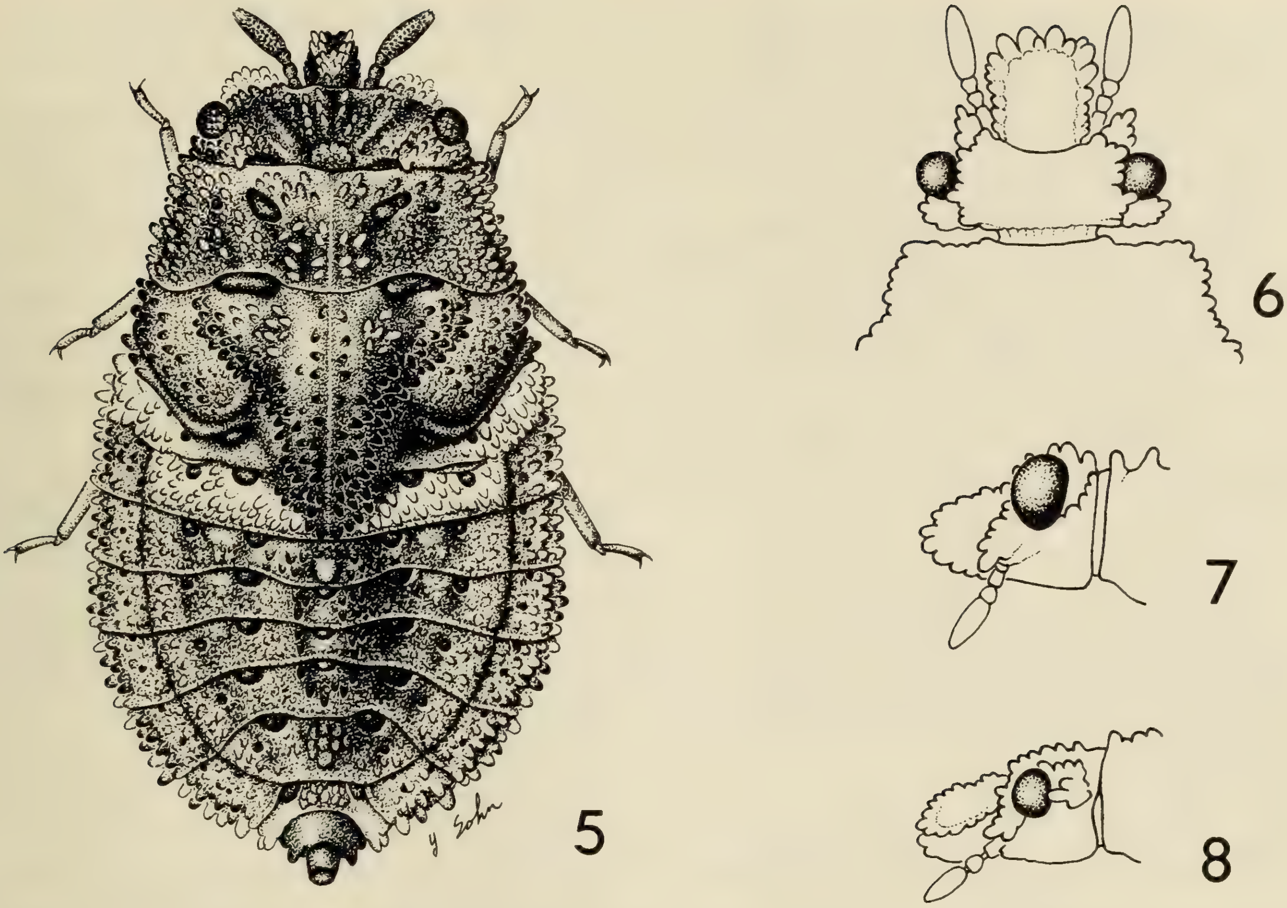
Distribution.—Dominican Republic (fossil in amber).

Etymology.—This new species is dedicated to Jacob Brodzinsky and his wife Marienela Lopez-Penha Brodzinsky in recognition of their realization of the scientific value of the amber collection and their assuring its availability for future students by permitting it to come to the Smithsonian Institution.

Calisiopsis kormilevi, new species
Figs. 2, 5, 7

Diagnosis.—This new species differs from all other known species in the genus by the combination of the presence of an irregular longitudinal row or prominent pale tubercles on each side of scutellar disc plus the interocular area of the head, including the midline, being strongly depressed below the upper margins of the eyes.

Description.—Holotype ♂, ovate, length 3.0, maximum width 1.45. Aspect generally characteristic for the genus with tubercles on head, in 4 discal rows on pronotum, and along margins on pronotum, abdomen, and scutellum. Head broader than long, 0.84:0.58; interocular area, including midline, depressed considerably below upper level of eyes, latter appearing strongly, obliquely elevated; anterior lobe with numerous irregularly placed, very short tubercles, dorsal outline pointing at or very slightly below midheight of eye (Fig. 7). Antenna about two-thirds as long as head, segments I–III very short (each 0.12 long), moniliform; segment IV as very slightly longer (0.40) than I–III combined, bearing numerous small pale dots.



Figs. 5–8. 5. *Calisiopsis kormilevi,* new species, nymph, natural length 2.5; 6. *Calisiopsis planiceps* Kormilev, dorsal view of head; 7. *Calisiopsis kormilevi,* new species, lateral view of head; 8. *Calisiopsis minuta* Kormilev, lateral view of head.

Pronotum broader than long, 1.24:0.58; anterior margin transverse, collar narrowly projecting; posterior margin feebly bisinuate, broadly but shallowly convex medially. Scutellum with usual tubercle-bearing, strong, triangular elevation at middle base, midline beyond it with a row of short, prominent tubercles; disc each side of midline, half way to lateral margins, with an irregular longitudinal row of 5–6 prominent pale tubercles. Wings, except sclerotized costa, concealed under scutellum.

Connexival segments and their laterotergites exposed, the latter sloping upward to an inner edge which is not differentiated as a vertical rim (as it is in *C. brasiliensis* where it forms a continuous pale rim).

Abdomen without tubercles on ventral surface.

Color: Dark dull brown with interocular area of head, anterior lobe and humeri of pronotum paler brown; scutellum extensively marked with yellow (large oblique area in each basal angle, thence irregularly distributed). Most tubercles yellow, but black on dorsum of anterior lobe of head, along constriction of scutellum, and in middle of lateral edge of connexival segments. Tibiae and apices of femora yellow.

Holotype ♂.—Peru: Madre de Dios, Manu Pakitza, Rio Manu, 250 m, 12°7′S, 70°58′W, 22 Sep 88, Zone 02/18/08, Tree 12 *Matisia cordata,* Tree 13 *Hirtella triandra,* Insecticial Fogging, Erwin and Farrel colls, deposited in the Museo de Historia de Lima, Lima, Peru. Paratypes: 25 ♂ 6 ♀, 10 nymphs, same data as holotype, in that institution and in the National Museum of Natural History, Washington, D.C.

Comments.—The above description applies well to the paratypes except in the scutellar coloration: all show the large, oblique yellow mark in the basal angles of the scutellum but exhibit considerable variation of the amount of pale markings on the remainder of the scutellar disc.

Distribution.—Peru.

Etymology.—This species is dedicated to Nicholas A. Kormilev whose 142 papers on the taxonomy of the flat bugs greatly advanced our knowledge of the Aradidae.

Calisiopsis minuta Kormilev

Calisiopsis "*minutus*" Kormilev, 1959a:221 [new species: Mexico].

Diagnosis.—This is the only member of the genus having the median area of the head higher than the dorsal margin of the eye and the outline of the anterior head lobe directed above the eye.

Distribution.—Mexico.

Calisiopsis nigrotuberculata, new species

Fig. 3

Calisiopsis ampliceps.—Kormilev, 1959a: 221.

Diagnosis.—The rather regular row of blackened tubercles each side of the scutellum's median carina provides a convenient separation of this species from all others in the genus.

Description.—Holotype ♀ ovate, length 3.4, greatest width 1.6. Aspect typical for genus with prominent tubercles on head, in four longitudinal rows on pronotal disc, along lateral margins of pronotum, abdomen, scutellum, and connexival laterotergites, and in a slightly irregular, longitudinal row on each side of median carina of scutellum.

Head: Wider than long, 0.80:0.58; interocular area depressed each side of median line, latter as high as eyes. Antenna about two-thirds as long as head; segments I–III very short (0.14:0.10:0.12), almost moniliform, their combined lengths slightly less than length of segment IV (0.40), latter fusiform, with small yellow dots (right antenna with segments III–IV missing). Anterior lobe laterally with very low (shorter than wide) tubercles forming a regular dorsolateral row and an irregular lateral row. Anterior lobe with dorsal outline directed at upper margins of eyes.

Pronotum wider than long, 1.96:0.64. Anterior margin transverse, collar very slightly projecting; posterior margin broadly, shallowly bisinuate.

Scutellum with mediobasal elevation bearing three prominent tubercles laterally, midline behind elevation with a slight but distinct carina topped with a row of small tubercles; disc each side of midline with an almost straight row of elevated, darkened tubercles.

Connexival segments and their laterotergites exposed, latter mesally sloping abruptly upward to form a continuous rim.

Abdomen: Ventrally without tubercles.

Color: Brown; scutellum subbasally and subapically with pale areas, the latter less distinct, reaching to margin. Tubercles, except those along median of head, medioapically on pronotum, on elevated scutellar base, and row along posterior margin of each connexival segment, concolorous brown.

Holotype ♀.—"SLP Mex[ico], Lar[edo], Tex[as]. 55540, 5-23-55-5495, with orchids. *Calisiopsis ampliceps,* Det. N. A. Kormilev 957." Deposited in the National Museum of Natural History, Washington, D.C.

Comment.—Although the specimen with the data reported by Kormilev (1959a:221) was not found, the specimen used here (one intercepted on Mexican orchids being transported into Texas) presents no important differences from his description of *C. ampliceps* given there.

Distribution.—Mexico.

Etymology.—The species name is given to direct attention to the longitudinal row of black tubercles on the scutellum each side of its median carina.

Calisiopsis planiceps Kormilev
Fig. 6

Calisiopsis planiceps Kormilev, 1976:69 [new species: Brazil].

Diagnosis.—The presence of a single row of long spines radiating out from the free margins of the anterior lobe of the head (Fig. 6) marks this species distinct from all others in the genus.

Distribution.—Brazil.

Acknowledgments

Appreciation is expressed to W. R. Dolling, of the British Natural History Museum, for loan of the types of *Calisiopsis ampliceps* from that institution; to T. J. Henry, U.S. Department of Agriculture, for safely hand-carrying those specimens to me; to T. L. Erwin for permission to examine specimens taken during the canopy survey by the Biolat Program of the National Museum of Natural History (Smithsonian Institution) in Peru; to Y. T. Sohn, Smithsonian illustrator, for the excellent illustrations; to Ms. S. B. West, Smithsonian secretary, for aid in preparing the final manuscript; to O. S. Flint, Jr., T. J. Henry and T. Vasarhelyi for careful and helpful reviews of the manuscript; and to G. Steyskal for pointing out that the ending *-opsis* is feminine.

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A NEW GENUS AND SPECIES OF STYGOBIONTIC DRYOPID BEETLE, *STYGOPARNUS COMALENSIS* (COLEOPTERA: DRYOPIDAE), FROM COMAL SPRINGS, TEXAS

Cheryl B. Barr and Paul J. Spangler

Abstract.—A stygobiontic new genus and species, *Stygoparnus comalensis,* from Comal Springs, Texas, is described and compared with the dryopid genus *Helichus.* Distinctive characters of the adult and larva are illustrated with pen and ink drawings and scanning electron micrographs. This new taxon is the first member of the family Dryopidae reported from subterranean waters.

Most aquatic entomologists agree that our present aquatic insect fauna evolved from terrestrial taxa (Ross 1965, Wooton 1972, Resh & Solem 1984). Among the 22 families of aquatic and semiaquatic beetles known from the Western Hemisphere, there are two, Torridincolidae and Noteridae, that are known to be aquatic in all stages. In some of the other families, the adults are terrestrial and their larvae aquatic, while in others the reverse is true. There are taxa with stages that are terrestrial, semiaquatic, or aquatic in families like the Hydrophilidae. The hydrophilids are sometimes cited as examples of taxa derived from terrestrial progenitors (Crowson 1960, 1981; Miller 1963).

Evidence is accumulating that Western Hemisphere members of the family Dryopidae also show an evolutionary sequence similar to that of the hydrophilid beetles. Previously, the only known aquatic dryopids were the adults of the genera *Elmoparnus* Sharp, 1882, *Helichus* Erichson, 1847, and *Postelichus* Nelson, 1989; and the known larvae of the three genera were reported to be terrestrial (Doyen & Ulrich 1978, Spangler 1981, Ulrich 1986). Adults of the dryopid genera *Guaranius* Spangler, 1991, *Holcodryops* Spangler, 1987, *Protoparnus* Sharp, 1883, *Quadryops* Perkins & Spangler, 1985, *Sostea* Pascoe, 1860, and *Sosteamorphus* Hinton, 1936b, are known only from terrestrial habitats. The larvae of these genera are unknown but presumed to be terrestrial. Adults of *Dryops* Olivier, 1791, *Pelonomus* Erichson, 1847, and *Onopelmus* Spangler, 1980, are known riparian taxa usually found on rocks and vegetation above water at the air-water interface. Larvae of *Dryops* and *Pelonomus* are reported to be terrestrial (Hinton 1936a, 1955; Chandler 1956; Berjon 1964; Brown 1991), and those of *Onopelmus* are presumed to be terrestrial (Spangler 1980).

The world fauna and characteristics of aquatic stygobiontic beetles were reviewed by Spangler in 1986. He reported 16 species in the families Dytiscidae, Elmidae, Hydrophilidae, and Noteridae. *Stygoparnus comalensis* is the world's first known stygobiontic member of the Dryopidae.

Habitat and Fauna

The Edwards Aquifer (Balcones Fault Zone) of central Texas is a vast underground storehouse of water fed by streams from the south and west. Water is "captured" as recharge by the aquifer when surface streams cut across the highly porous and fractured Edwards Limestone formation. The water then emerges as artesian springs along the Balcones Escarpment. The aquifer is believed to contain extensive water-filled caverns and caves (Pettit & George 1956, Klemt et al. 1979).

The Comal Springs complex in New Braunfels is the largest in Texas and discharges a mean historic flow of about 300 cubic feet per second (cfs) (8.31 cubic meters per second [cms]) (Ogden et al. 1986). The springs emerge at an elevation of 190 m from the Comal Springs fault along the base of a steep bluff that marks the edge of the Balcones Escarpment. Most of the water enters the aquifer as much as 100 km to the west; faulting has hydrologically isolated Comal Springs from any large sources of local recharge (Brune 1981, Pearson et al. 1975, Rothermel & Ogden 1987). This water may flow through the aquifer at depths as great as 150 m before surfacing at the springs (Brune 1981). Four main spring orifices, Comal 1–4 (j, k, l, b; Brune 1981) have been identified and hydrologically monitored by the Edwards Aquifer Research and Data Center (EARDC). Several minor outlets are also present. The Comal 1, 2, and 3 orifices are located in city-owned Landa Park, The spring runs, confined by concrete and rock walls, flow into Landa Park Lake, which is the headwaters of the Comal River. Increasing withdrawal of ground water has caused decreasing spring flow in recent years. Modeling has predicted that Comal Springs, as well as nearby Hueco and San Marcos springs, will permanently go dry as early as the year 2020 (Klemt et al. 1979).

The Edwards Aquifer is one of the most diverse subterranean aquatic ecosystems in the world in terms of richness of troglobitic species (Longley 1981, 1986). Forty-two species and/or subspecies of stygobiontic animals have previously been described from the artesian zone (Hershler & Longley 1986). Of these, the only insect is the stygobiontic dytiscid beetle *Haideoporus texanus* Young & Longley, 1976, from a well in San Marcos, the larva of which was described by Longley and Spangler (1977). *Heterelmis comalensis* Bosse, Tuff, & Brown, 1988, an elmid beetle from Comal Springs, is believed to be endemic but not stygobiontic.

The senior author visited Comal Springs on four separate occasions. All four major orifices and two smaller outlets near Comal 4 were sampled (Fig. 1), but *Stygoparnus comalensis* was found only at Comal 2 springhead and associated run (Fig. 2). Nearby Hueco and San Marcos springs were also sampled without success. Likewise, other collectors have found *S. comalensis* only in Comal 2 and run. The adult beetles were all taken in the upper third to fourth of the spring run (Fig. 2); most specimens were collected from the headwater outlets (Figs. 3, 4) or from outlets beneath either bank (Fig. 5), but a few were taken from mid-stream. The larvae were collected from some of the same outlets; but because they are thought to be terrestrial, the microhabitat is presumed to be the ceilings of the orifices. Water covered only part of the openings and soil, roots, and debris were exposed above the water line (Fig. 5); some of the material was dislodged while sampling.

The substrate of the spring outlets and run consists of coarse sand and angular rock fragments. When sampled by the senior author, the water was clear and ranged from about 5–31 cm deep. As monitored from September 1982 to July 1984 by the EARDC, water parameter ranges included the following: daily discharge, 1.3–8.2 cfs; water temperature, 22.6–24.6°C; dissolved oxygen, 3.1–5.5 ppm; and pH, 6.88–8.81 (Ogden et al. 1985a, 1985b).

Stygoparnus, new genus

Type species.—*Stygoparnus comalensis*, new species.

Diagnosis.—*Stygoparnus* may be distinguished readily from all other described dryopid genera by its vestigial eyes and 8-segmented antennae.

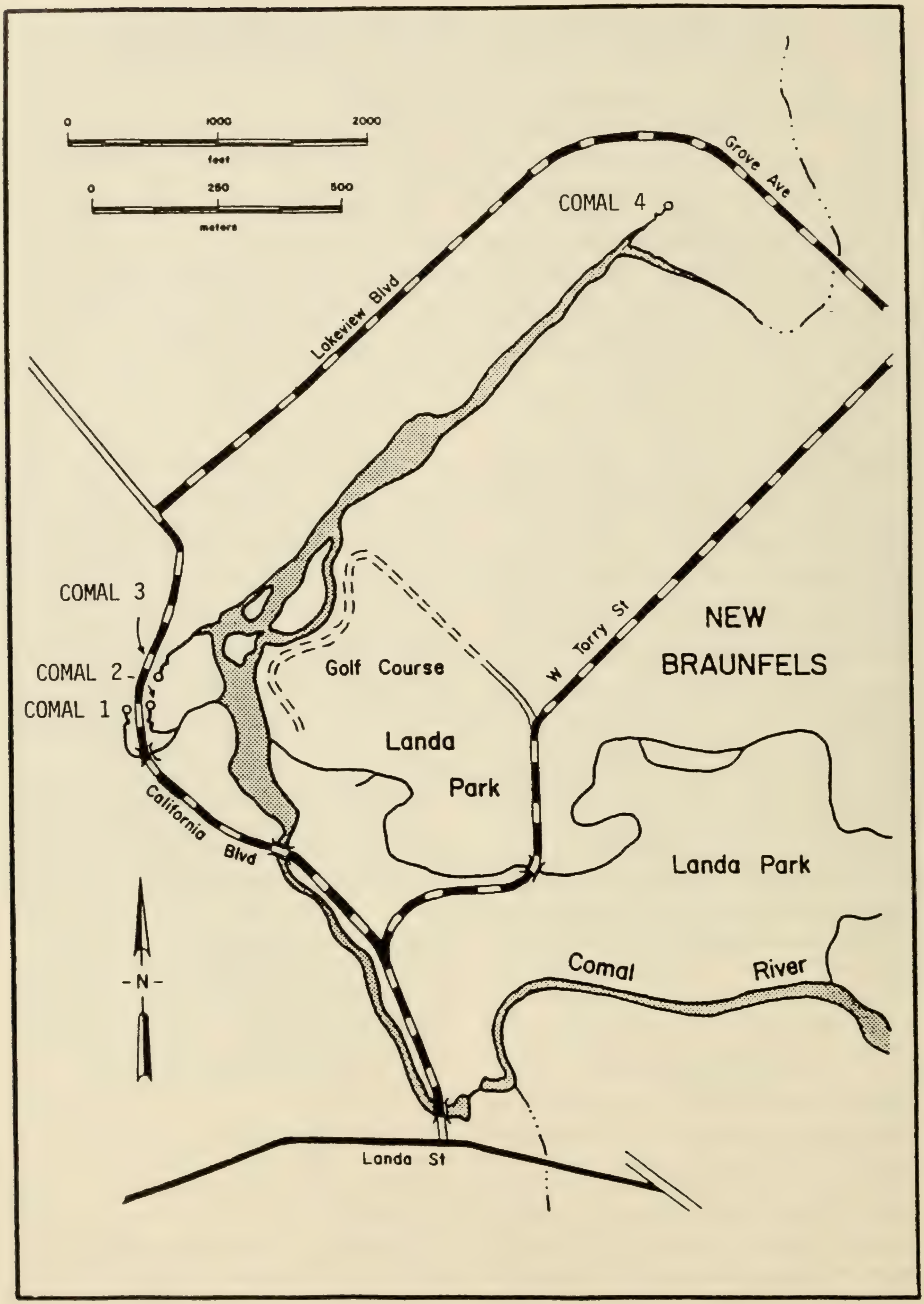
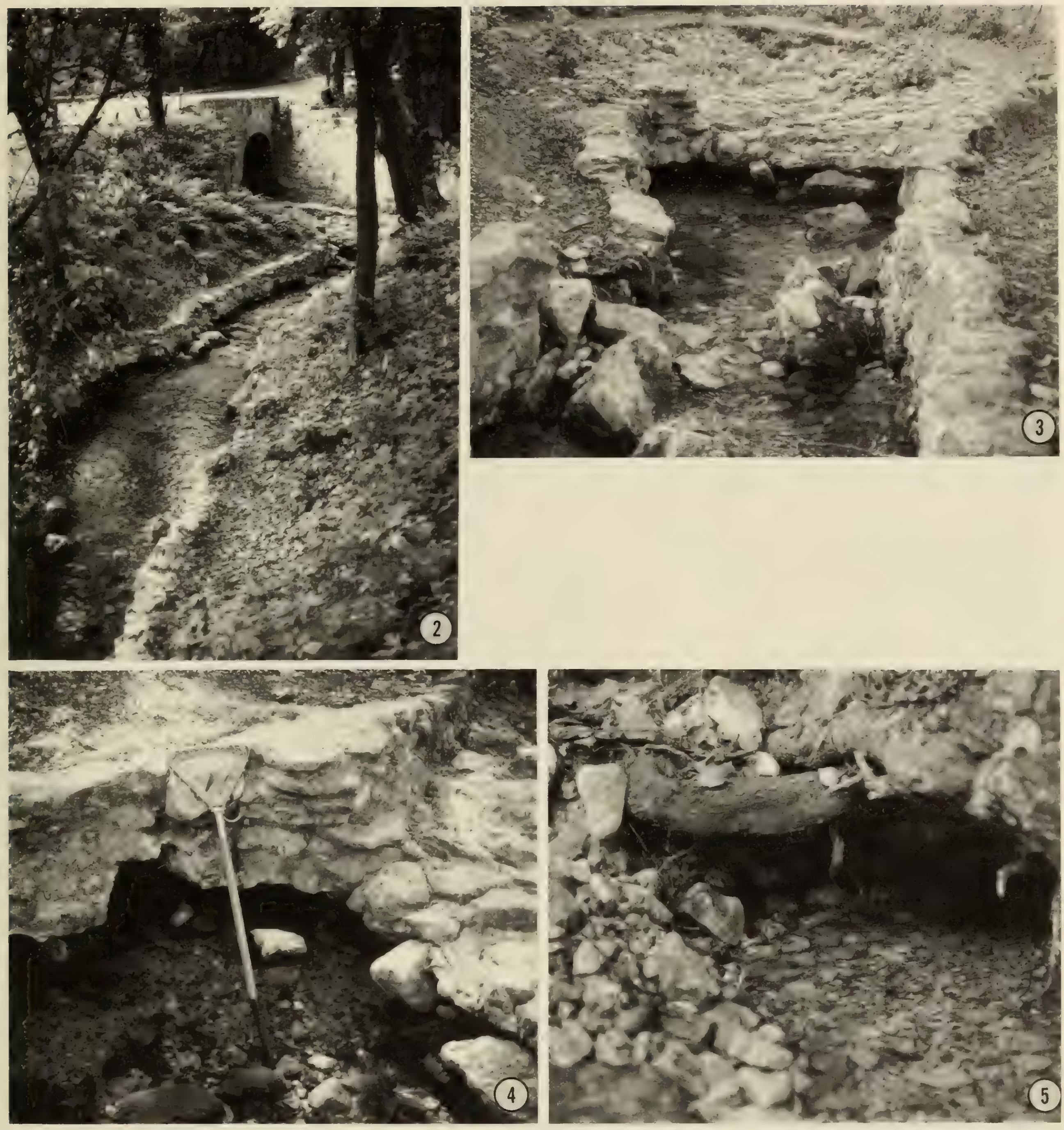


Fig. 1. Location of sampled orifices of Comal Springs, New Braunfels, Texas (from Ogden et al. 1985a).



Figs. 2–5. *Stygoparnus comalensis,* new genus, new species, biotope; Comal 2 springhead and run, Comal Springs, New Braunfels, Texas (photo by W. D. Shepard): 2, springhead and run; 3, springhead; 4, springhead, with aquatic net for scale; 5, spring outlet with ceiling exposed to air.

Adult (Figs. 6, 8–10).—Body form oblong, slender; depressed dorsally, convex ventrally. Cuticle thin, translucent. Indumentum of inconspicuous, fine, recumbent setae and plastron setae. Head retractile, slightly depressed dorsally. Eyes vestigial, reduced to several minute ocellus-like structures (Figs. 11, 17–19). Antenna, 8 segmented (Fig. 7); fitting into shallow acetabula; basal segment small, subtriangular; segment 2 large, trapezoidal, shield-like, covering and enclosing pectinate segments 3–8. Clypeus expanded laterally beneath antennal insertions. Maxillary palpus, 4 segmented; apical segment cylindrical, about 2 times as long as combined length of basal 3 segments. Apicolateral sensory pit on last segment of maxillary palpus ovoid, not

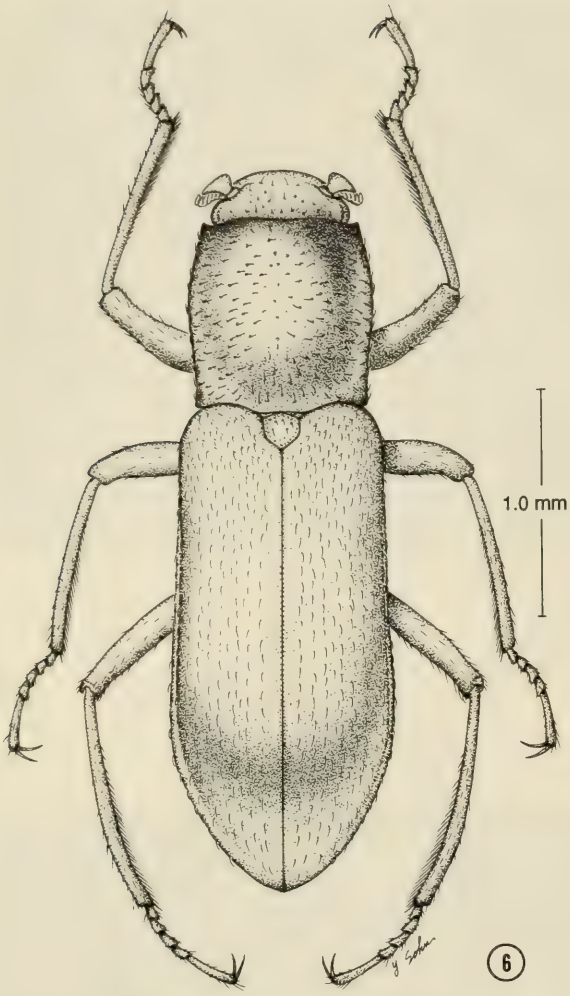


Fig. 6. *Stygoparnus comalensis,* new genus, new species, male: habitus, dorsal view.

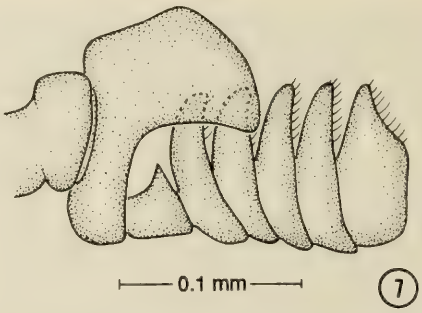
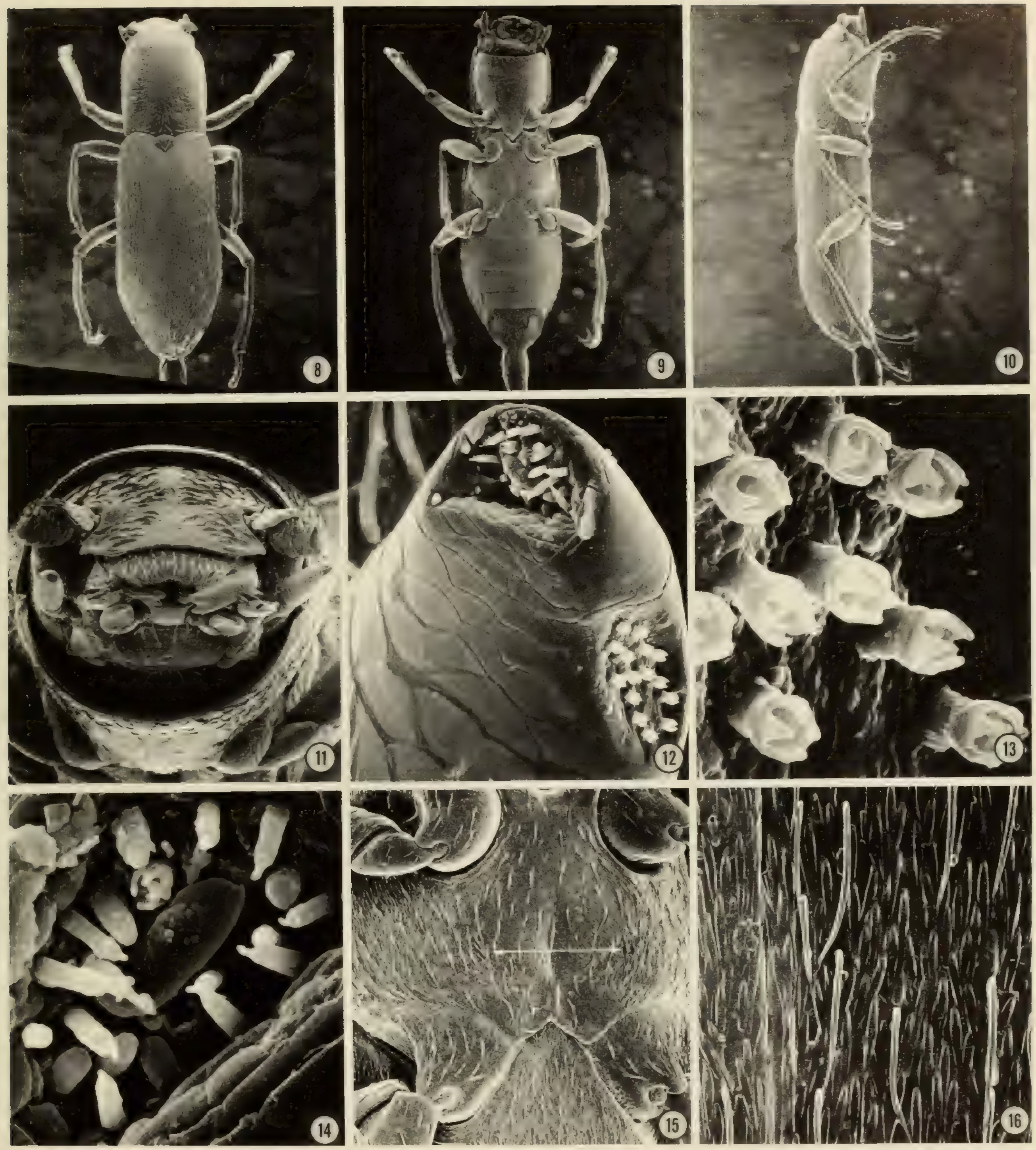


Fig. 7. *Stygoparnus comalensis,* new genus, new species, male: antenna, oblique view (to show segments).

deeply invaginated (Figs. 12–14). Labial palpus, 3 segmented; apical segment subovoid, slightly longer than combined length of basal 2 segments and broad, about 2 times as wide as penultimate segment (Fig. 18). Pronotum rectangular and slightly depressed, without sulci or carinae; anterior margin subtruncate; lateral margins smooth; prescutellar emargination well developed (Fig. 17). Scutellum large. Elytra wider at base than base of pronotum, depressed, without prominent punctures or striae; each elytron with shallow lateral groove extending from humerus to apex. Metathoracic wings vestigial, between ⅓ to ½ length of elytra (Figs. 20, 21). Prosternum long in front of procoxae. Prosternal process broad; apex angulate, slightly recurved, fitting into deep mesosternal fovea. Suture between mesosternum and metasternum indistinct. Metasternum with discrimen not extending onto intercoxal process, crossed by short transverse sulcus just anterior to metacoxae (Fig. 15). Each pair of coxae about equally transversely separated. Metacoxae deeply dividing abdominal sternum 1. Legs long, slender; middle leg shortest, hind leg longest. Femora moderately expanded, shorter than tibiae. Tarsal formula, 5-5-5. Last tarsal segment about as long as combined length of 4 preceding segments. Tarsal claws rather slender, without teeth. Abdomen of 5 visible segments; sterna decreasing in length toward apex except apical sternum as long as combined length of 2 preceding sterna. Apical sternum without plastron setae.

Etymology.—*Stygoparnus,* from the Latin *Stygius* (of the Styx, a river in the Nether World); plus *parnus,* a generic name coined by Fabricius for a dryopid genus now a junior synonym of *Dryops* Olivier; gender masculine.

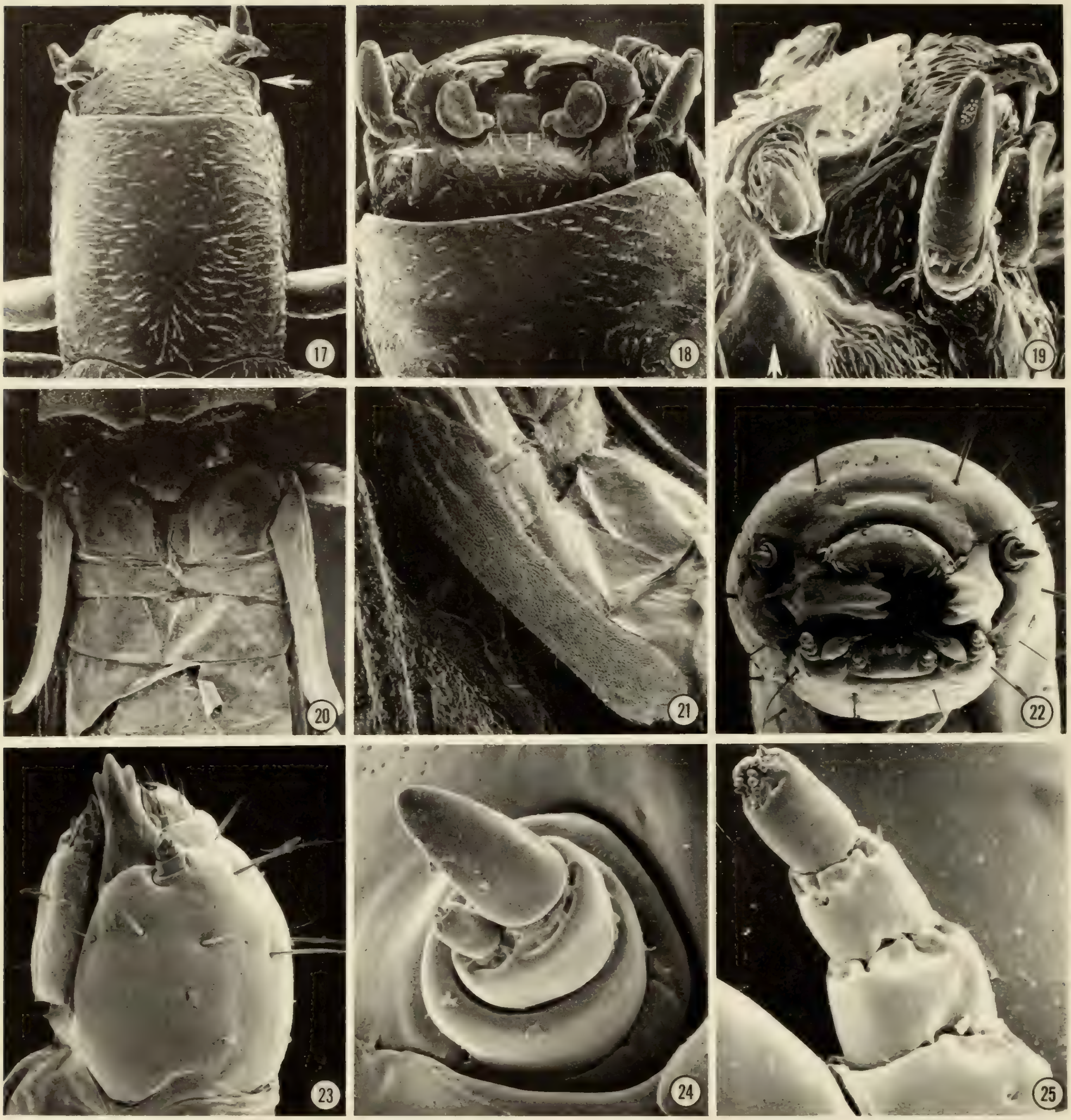
Larval diagnosis (late instar; by association).—Cylindrical, elateriform (Fig. 30). Light yellow brown. Head partially retracted into prothorax; hypognathous. Epicranial and frontal sutures complete (Figs. 31, 32). Antennae, 3 segmented (Figs. 24, 35). Stemmata absent. Mandible stout, with 3 blunt apical teeth; without mola or prostheca (Figs. 33, 34). Maxilla fused with labium; maxillary palpus, 4 segmented (Fig. 25); galea and lacinia separate, each with apical spines (Figs. 36, 37). Labium with palpiger and 2-segmented palpus. Prothorax as long as combined length of mesotho-



Figs. 8–16. *Stygoparnus comalensis,* new genus, new species, male: 8, habitus, dorsal view, ×30; 9, habitus, ventral view, ×30; 10, habitus, lateral view, ×30; 11, head and mouthparts, adoral view, ×120; 12, maxillary palpus, sensilla on apex of last segment, ×1700; 13, maxillary palpus, sensilla, and apicolateral pit, ×10,000; 14, maxillary palpus, sensilla, and apical pit, ×6000; 15, metasternum, discrimen and male setal tufts (arrows), ×130; 16, plastron setae on elytron, ×600.

rax and metathorax (Fig. 38). Legs short, 5 segmented. Spiracles peripneustic, functional; present on mesothorax and abdominal segments 1–8; spiracles on abdominal segment 8 on upper third. Abdominal segments 1–5 incomplete rings, parallel sided, without pleura; each segment with narrow sternal groove. Abdominal segments 6–8 complete sclerotized rings. Abdominal segment 9 tapering to a rounded apex; with operculum. Anal gills and hooks absent.

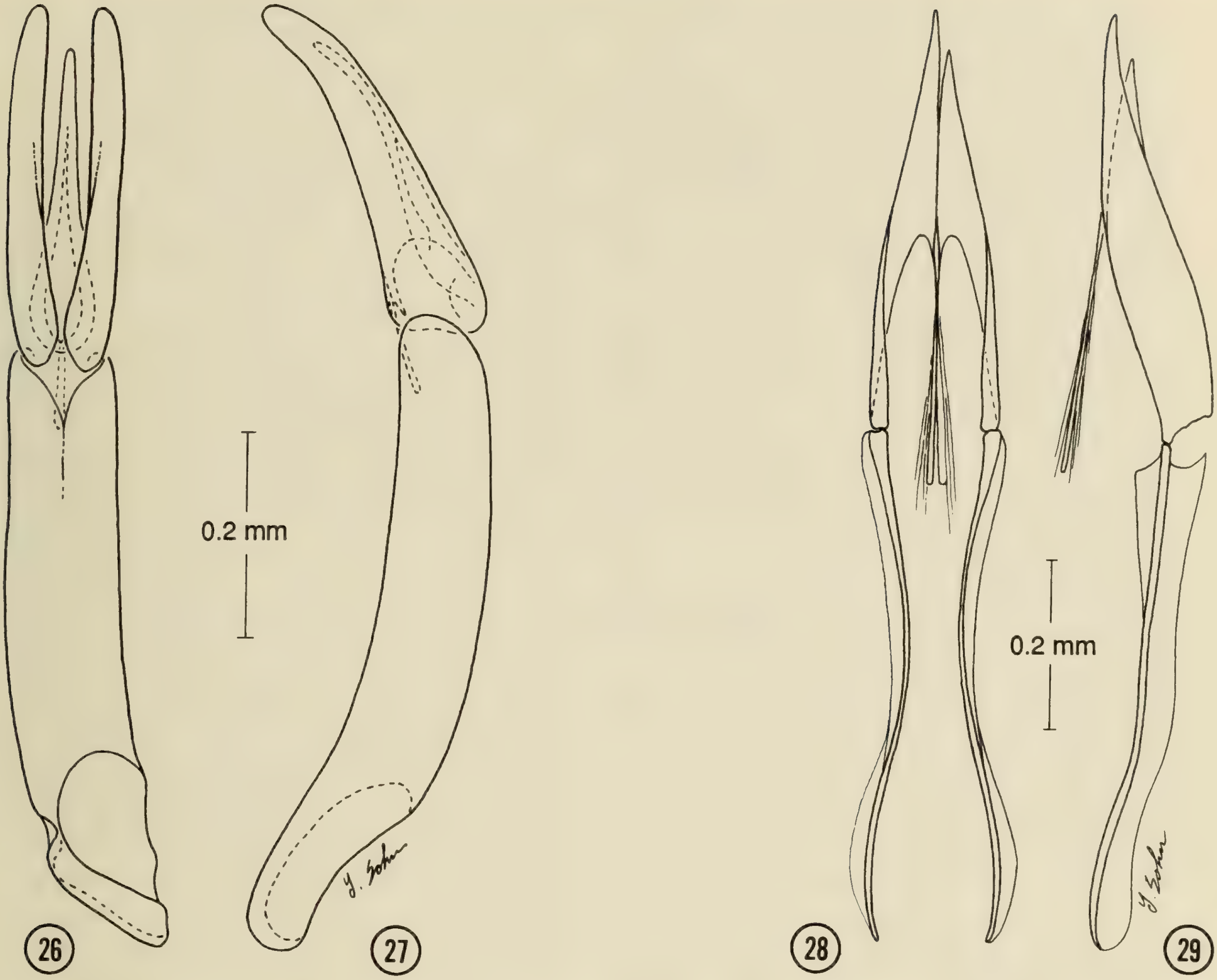
Comparative notes.—We consider *Sty-*



Figs. 17–25. *Stygoparnus comalensis,* new genus, new species: Figures 17–21, adult, male: 17, head, vestigial eye (arrow), and pronotum, ×80; 18, head, vestigial eye (arrow), ventral view, ×130; 19, head and vestigial eye (arrow), lateral view, ×270; 20, metathoracic wings, vestigial, dorsal view, ×80; 21, metathoracic wing, vestigial, lateral view, ×150. Figures 22–25, larva: 22, head, adoral view, ×170; 23, head, lateral view, ×170; 24, antenna, ×1300; 25, maxillary palpus, ×1400.

goparnus to be related to *Helichus* (Figs. 41–46) and they share the following synapomorphies (adults, 1–4): (1) adults aquatic; (2) last abdominal sternum without setae; (3) ventral surface densely and conspicuously granulate; (4) ovipositor long, bladelike (Figs. 28, 29); (5) larva with operculum rounded apically (Fig. 40).

Although we believe *Stygoparnus* is closely related to *Helichus, Stygoparnus* exhibits the following apomorphic character states not present in members of *Helichus* (adults, 1–5): (1) eyes vestigial (Figs. 11, 17–19); (2) antennae, 8 segmented (Fig. 7); (3) metathoracic wings vestigial (Figs. 20, 21); (4) discrimen extended only half length of



Figs. 26–29. *Stygoparnus comalensis,* new genus, new species: 26, male genitalia, dorsal view; 27, male genitalia, lateral view; 28, ovipositor, dorsal view; 29, ovipositor, lateral view.

metasternum (Fig. 15); (5) elytra without striae (Figs. 6, 8); (6) larva with lateral spiracles on abdominal segment 8 on upper third of segment (Figs. 30, 39).

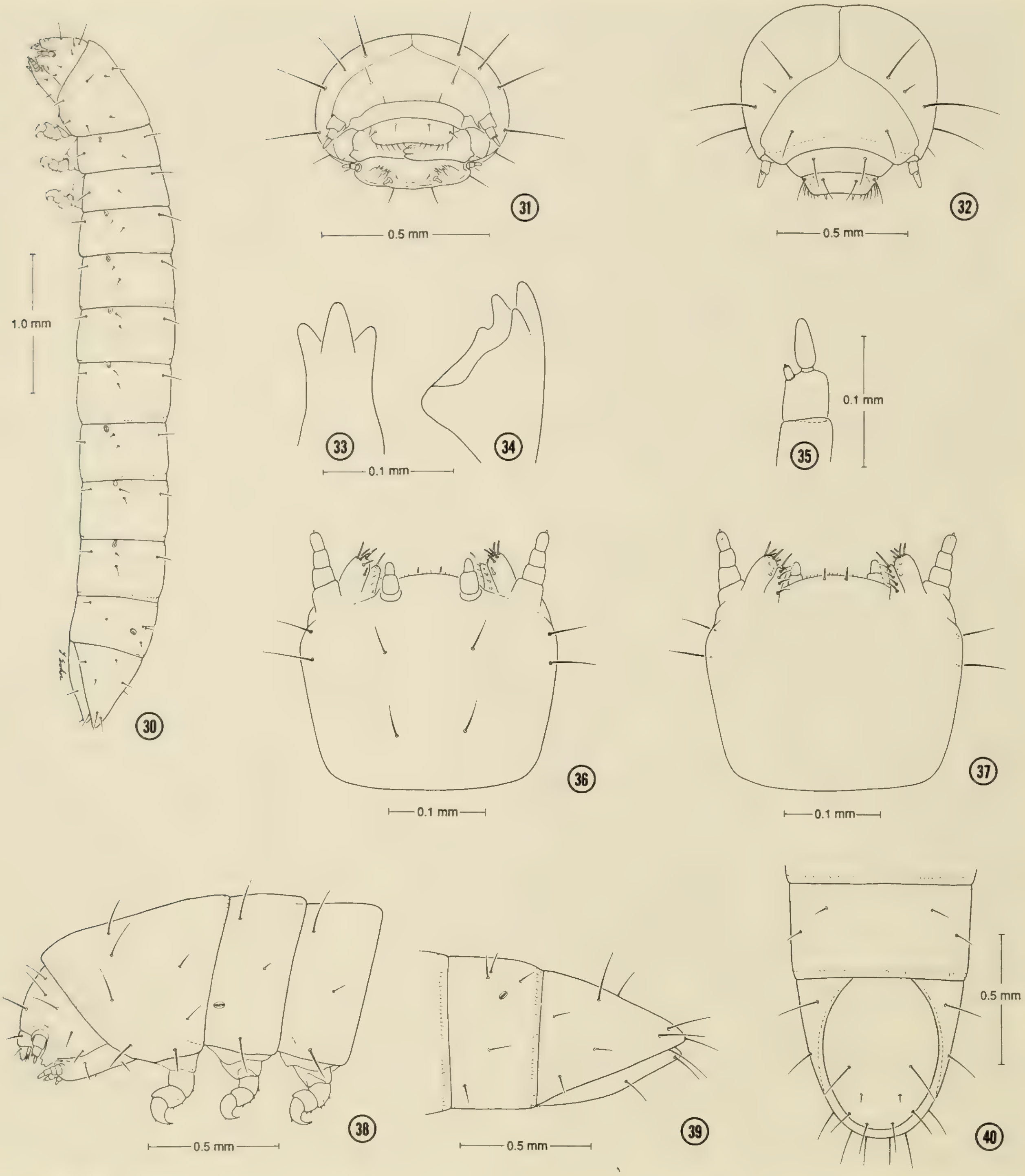
Stygoparnus comalensis, new species
Figs. 6–40

Holotype ♂.—Body form and size: Elongate, subparallel; depressed dorsally, convex ventrally. Length, 3.12 mm; width, 1.00 mm.

Color: Entirely reddish brown; cuticle thin and translucent.

Head: Moderately shining; finely punctate; punctures separated by 2 times diameter of puncture; each puncture bearing a medium long, fine, white seta. Eyes vestigial, reduced to minute, subcircular, unfaceted, ocellus-like structures (Figs. 11, 17–19, arrows). Clypeus expanded laterally; rather bare and shining medially, with few punctures; punctures becoming more dense laterally. Labrum densely pubescent, shallowly emarginate apically; anterolateral angles rounded.

Thorax: Pronotum 0.88 mm long, 0.85 mm wide; widest medially; anterior margin subtruncate; posterior margin trisinuate; anterolateral pronotal angles moderately acute (Fig. 17); posterolateral angles moderately acute; disc shining, with small punc-



Figs. 30–40. *Stygoparnus comalensis,* new genus, new species, larva: 30, habitus, lateral view; 31, head, adoral view; 32, head, frontal view; 33, mandible, ventral view; 34, mandible, lateral view; 35, antenna; 36, maxillolabial plate, ventral view; 37, maxillolabial plate, dorsal view; 38, head and thorax, lateral view; 39, abdominal segments 8 and 9, lateral view; 40, abdominal segments 8 and 9 and operculum, ventral view.

tures separated by about 5 times diameter of puncture; punctures adjacent to disc each bearing a fine white seta with apex directed toward meson; declivous margins covered by whitish plastron setae interspersed with elongate granules bearing fine, recumbent setae; prescutellar emargination present. Scutellum large, suboval; appearing hollow because of more darkly sclerotized margin. Elytra 2.28 mm long, 1.00 mm wide; humeral angles obtuse, not prominent; apicolateral margins deeply grooved to receive expanded lateral margins of last abdominal sternum; surface covered by whitish plastron setae interspersed with elongate granules bearing fine, recumbent setae (Fig. 16). Prosternum shining medially, with sparse setae and punctures; laterally with plastron setae and elongate granules bearing recumbent setae separated by 1 to 3 times granule width. Plastron setae especially evident on mesepisternum, mesepimeron, and metepisternum. Metasternum covered with plastron setae and elongate granules separated by 2 to 3 times granule width and each bearing a fine seta (Fig. 15). A tuft of fine, sparse, longer setae on each side of discrimen on metasternum (Fig. 15, arrows). Legs each with femur and tibia with fine setae and densely granulate. Femoral lengths: 0.75, 0.70, 0.87 mm. Tibial lengths: 0.88, 0.85 mm, 1.05 mm. Tibia with dense golden brown medial fringe of tomentum.

Abdomen: Sterna 1–4 with plastron setae interspersed with elongate granules separated by 2 to 3 times granule width and each bearing a fine seta. Apical sternum without plastron setae, shining; smooth basomedially, elsewhere punctures separated by puncture diameter and each bearing a fine seta; lateral margins moderately bent upward to clasp tips of elytra.

Genitalia: As illustrated (Figs. 26, 27).

Allotype.—Similar to male; length 3.12 mm, width 0.98 mm. Scutellum broader and more triangular. Metasternal tufts absent. Ovipositor as illustrated (Figs. 28, 29).

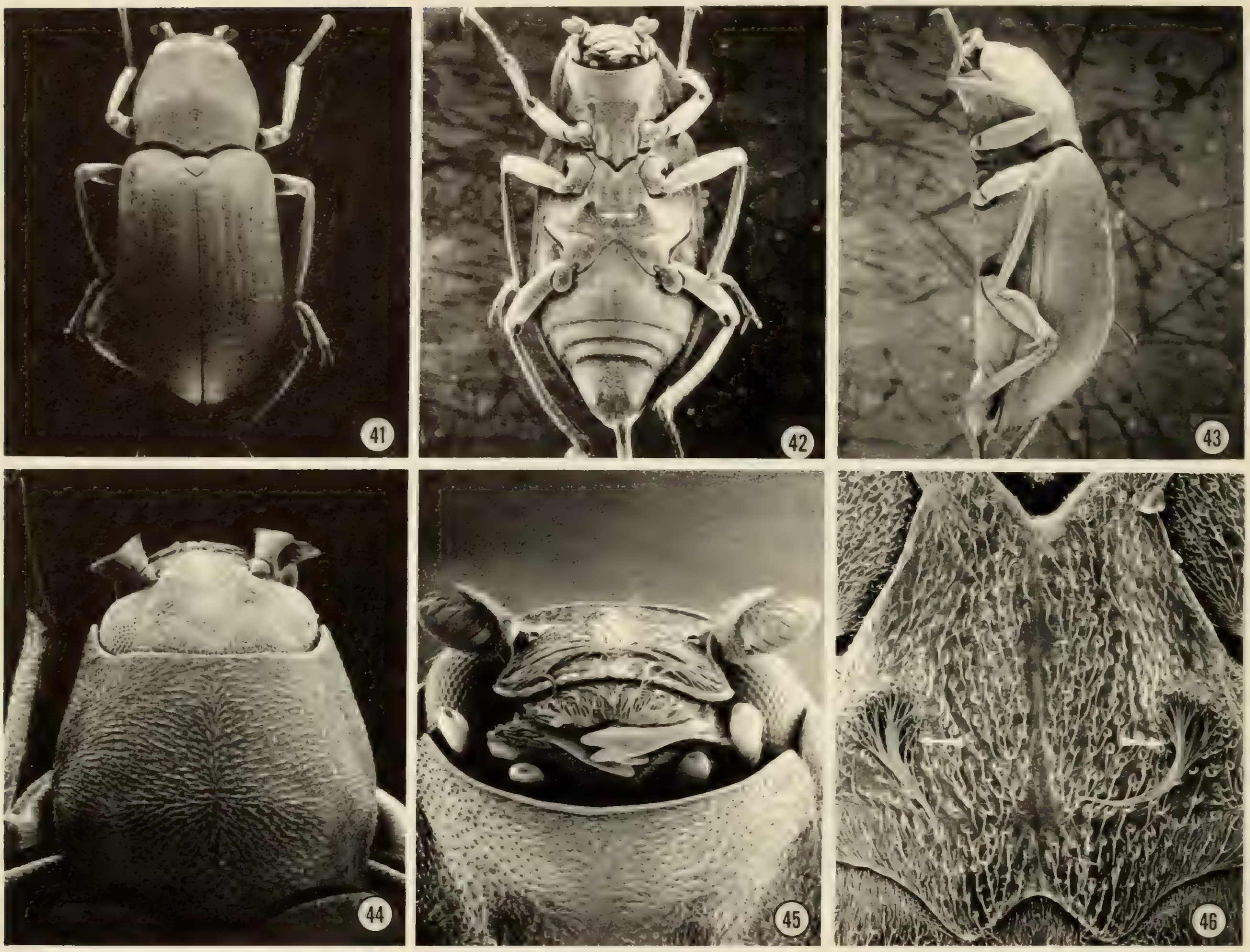
Variations.—Very little variation was noted among individuals. Males averaged slightly larger than females when measurements of 18 males and 13 females were compared: total length: ♂ 3.00–3.70 mm, ♀ 2.88–3.60 mm; width: ♂ 0.95–1.10 mm, ♀ 0.92–1.12 mm; pronotal length: ♂ 0.85–0.96 mm, ♀ 0.84–0.95 mm; pronotal width: ♂ 0.78–0.88 mm; ♀ 0.76–0.88 mm; elytral length: ♂ 2.08–2.40 mm, ♀ 2.00–2.40 mm.

Larva (late instar; by association).—Form and size: Cylindrical (Fig. 30). Length, 6–8 mm; width, 0.8–1.0 mm.

Color: Light yellow brown.

Head: Partially retracted into pronotum. Ovate in adoral and frontal view (Figs. 31, 32). Width about 1.2 times height; cranium with 5 setae in dorsoventral line on each half posteriad of epicranial suture; all setae curving laterally, 1 seta posteriad of and parallel to ventral seta. Gular suture indistinct. Frons with 2 setae positioned equally between meson and lateral margin; anteclypeal margin shallowly emarginate. Clypeus with width 4 times length; postclypeus sclerotized; anteclypeus membranous, with 4 setae. Antenna (Figs. 24, 31, 35) inserted anteriad of mandibles, directed ventrally; segment 1 about 1.5 times as wide as segment 2; segment 2 about 2 times as wide as segment 3 and shorter than segments 1 or 3; sensillae on segment 1, intersegmental membrane between segments 2 and 3, and antennal appendix; antennal appendix about 0.3 times length of apical segment (Fig. 24). Mandibles tridentate (Figs. 33, 34), wedge shaped; length 1.3 times width; mesal surface slightly concave; middle tooth longest; basal pigmentation brown, apex black; molar process absent. Maxillolabium a rectangular plate; dorsal surface glabrous medially, with 2 setae on anteromedial margin (Fig. 37); ventral surface glabrous except with 8 setae—1 at each base of labial and maxillary palpi, 2 near posteromedial margin, and 2 on anterolateral margin near bases of maxillary palpi (Fig. 36). Maxillary palpus (Fig. 25), 4 segmented; tapering toward apex; segments subequal in length; 1 or more cone shaped sensillae on each segment. Galea and lacinia distinctly separate. Galea lobate, directed slightly mesad, with a row of 6 spines on dorsoapical surface. Lacinia digitate, directed mesad; with a row of 5 apicomedial spines on dorsal surface. Labial palpus, 3 segmented; segments unequal in length; apical segment with width about 0.5 times width of penultimate segment and 3 or 4 sensillae on anteromedial margin.

Thorax (Fig. 38): Pronotum, along dor-



Figs. 41–46. *Helichus suturalis* LeConte, male: 41, habitus, dorsal view, ×20; 42, habitus, ventral view, ×20; 43, habitus, lateral view, ×20; 44, head, normal eyes, and pronotum, dorsal view, ×40; 45, head and mouthparts, adoral view, ×80; 46, metasternum, discrimen and male setal tufts (arrows), ×110.

somedian line, longer than combined length of mesonotum and metanotum; conceals head to dorsal arm of epicranial suture; with transverse row of setae at about anterior third, setae arising closer to anterior margin ventrally. Mesonotum rugose anteriorly, becoming glabrous posteriorly. Mesothorax with ventral, anterolateral spiracle. Metathorax similar to mesothorax but lacking spiracle. Legs similar. Prothoracic pair large; coxa dome shaped, slightly wider than long; trochanter longer on posterior surface than on anterior surface; femur slightly longer and broader than tibiotarsus; tibiotarsus tapering apically; pretarsus sclerotized, pigmented apically; claw robust, curved.

Abdomen: Glabrous. Segments 1–9 with anterior dorsal margins without rows of ridges; intersegmental membranes striolate. Sterna 1–5 narrow, folded, membranous or lightly sclerotized, fused with pleurites, forming incomplete rings, with narrow sternal groove. Terga 6–8 fused ventrally, forming rings. Segment 8 (Fig. 39) with dorsal surface slightly longer than ventral surface; lateral surface with 3 long setae above and 2 long setae below level of spiracle. Spiracles present on lower third of segments 1–7 (Fig. 30) and on upper third of segment 8 (Fig. 39). Segment 9 (Fig. 39) with 6 long lateral setae on each side; apex subacute in lateral view; dorsal surface striolate along anterior margin. Operculum covering cloacal chamber; with 4 long setae on posterior margin, 2 long setae slightly posteriad of midlength, and 2 short setae equidistant from meson and lateral margins (Fig. 40). Anal gills and abdominal hooks absent.

Type data.—Holotype ♂: United States: Texas: Comal County, New Braunfels, Landa Park, Comal Springs, Comal 2 springhead/run, 2 May 1988, C. B. Barr; deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Allotype: Same data as the holotype.

Paratypes: Fifty-one adults and 6 larvae, all from same locality as holotype: 25 Apr 1987, H. P. Brown, 3 adults; 1 Aug 1987, C. B. Barr, 2 adults; 23 Apr 1988, H. P. Brown, 7 adults; 28 Apr 1988, C. B. Barr, 7 adults, 1 larva; 2 May 1988, C. B. Barr, 10 adults, 3 larvae; 6 Jun 1988, W. D. Shepard, 22 adults, 2 larvae. Paratypes will be deposited in the following collections: American Museum of Natural History, New York, New York; California Academy of Sciences, San Francisco, California; Canadian National Collection, Ottawa, Canada; Louisiana State University Insect Collection, Baton Rouge, Louisiana; Muséum National d'Histoire Naturelle, Paris, France; Natural History Museum, London, England; Oklahoma Museum of Natural History, Norman, Oklahoma; Texas Agriculture and Mechanical University, College Station, Texas; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and the private collections of C. B. Barr and W. D. Shepard.

Etymology.—Named for Comal Springs, Texas, the type locality.

Laboratory Observations

Ten live beetles were brought back to the laboratory to observe their behavior. They were kept in a glass bowl, 20 cm in diameter and 7 cm deep, on a substrate of small rocks taken from Comal Springs. Water filling the bowl also came from the springs; as it evaporated, it was replaced with distilled water. A small aquarium pump and bubblestone provided aeration.

Stygoparnus comalensis seems to be rather fragile as a result of being lightly sclerotized. Three beetles died within about 2 weeks, and only one survived longer than four months. Most had visible trauma or damage of some type (i.e., missing tarsal claws, legs, or antennae; cuticle punctures; etc.). The single survivor lived for 21 months, and it appears that its death was caused by the sudden addition of large amounts of new water.

Although the beetles rested and crawled on all surfaces of the rocks, most of their time was spent on the sides or undersides. A couple of individuals spent a notable amount of time just below the air-water interface on rocks that projected out of the water. In one instance, a beetle was observed totally above water for a few minutes atop a wet rock. Beetles were often seen grazing on the rock surfaces. Small amounts of leaf litter taken from the springs were periodically added to the bowl, but the beetles were not observed feeding on the fragments.

The most interesting behavior, noted once, was what might have been a plastron grooming procedure. A beetle just below the surface lifted its head and pronotum through the film, and re-submerged with a bubble of air encasing the mouthparts and a separate bubble between the pronotum and elytra. It then made chewing-type motions, passed both middle legs into and through the bubbles, and rubbed the legs down the sides of the body; this act was repeated multiple times. This particular beetle had very sparse plastron setae. The development and extent of the area of plastron setae seemed to vary among individuals. The plastron setae probably had been abraded in some individuals.

Discussion

The discovery of a troglobitic dryopid raises many questions. Most puzzling is the fact that the subterranean habitat must be amenable to both the aquatic adults and the larvae that are believed to be terrestrial. Where is the population centered and what is its geographic extent? Why has a supposedly hypogean beetle been found in an epigean habitat? Where do the larvae develop and pupate? Because we know little of the natural history of *Stygoparnus,* we can only hypothesize about the answers. Perhaps the population is concentrated in an underground cavern not far from where the springs issue, or maybe it dwells just below the surface because of the limitations of the immature stages. The occurrence of the beetles at the surface could be due to the amount of spring flow or availability of food resources. It has been hydrologically determined that the individual orifices at Comal Springs are fed by more than one flow path (Ogden et al., 1986). This may explain why the species has not been found in any of the other spring orifices, especially Comal 1 and 3 that are in close proximity (Fig. 1).

Acknowledgments

We are especially indebted to Harley P. Brown, University of Oklahoma, Norman, who first collected this species and directed the senior author to the type locality. David Whatley, Director of Parks and Recreation for the City of New Braunfels, Texas, is thanked for providing background information and granting permission to collect at Comal Springs in Landa Park. Dr. Glenn Longley, Director of the Edwards Aquifer Research and Data Center in San Marcos, Texas, was instrumental in providing resource information and data on the aquifer and associated springs.

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TWO NEW CRABS, *HOMOLOPSIS WILLIAMSI* AND *HOMOLOPSIS CENTURIALIS* (CRUSTACEA: DECAPODA), FROM THE WESTERN INTERIOR CRETACEOUS OF THE UNITED STATES

Gale A. Bishop

Abstract.—A single specimen representing a new species of a Cretaceous homolid crab occurs in the *Linuparus* faunal association of the Turonian Carlile Shale on the northern and eastern flanks of the Black Hills Uplift in South Dakota and Wyoming. *Homolopsis williamsi* is characterized by a quadrate, relatively flat carapace with well-developed grooves and prominent tubercles on the posterolateral margins. The specimen is preserved as an internal carapace steinkern enclosed in an apatite concretion associated with shell fragments of the bivalve mollusk *Inoceramus.* Another specimen representing a second new species of homolid crab was collected from the Heart Tail Ranch decapod association of the mid-early Campanian Gammon Ferruginous Member of the Pierre Shale on the northern flank of the Black Hills Uplift in Butte County, South Dakota in 1989. This new species, *Homolopsis centurialis,* is characterized by a more typical quadrate carapace with well defined grooves and tumid lobes surmounted by boss-like protuberances. The specimen is preserved in an apatite concretion in which the sides of the crab are somewhat splayed outward by vertical compaction. Review of the stratigraphic and geographic distribution of *Homolopsis* shows a pattern of development along the northern margin of the Tethys Seaway in western and northern Europe as well as in Australia during the Early Cretaceous and immigration into, and evolution in, the opening Atlantic and flooded Western Interior seaways of North America and northern Europe during the Late Cretaceous.

The apatite-preserved, decapod-rich fauna of the Pool Creek Shale Member of the Carlile Shale described by Bishop & Williams (1986), consists of the lobsters *Linuparus canadensis* (Whiteaves 1885), undescribed species of *Hoploparia,* and *Palaeonephrops,* and the crabs *Necrocarcinus olsonorum* Bishop & Williams, 1991, and *Homolopsis williamsi,* new species, in association with abundant worm, bryozoans, bivalves, cephalopods, vertebrates, and a few other taxa. The decapod assemblage is confined vertically to 3 m of shale, preserved in burrowed and pelleted apatite concretions, and has been traced continuously along strike for approximately 117 km, and down dip for 8 km, a distribution of at least 936 km^2. The Carlile Shale *Linuparus* assemblage represents the preserved fraction of an opportunistic decapod-worm association which periodically appeared in the Western Interior Cretaceous in response to mass killings and nutrient rains onto the substrate surface (Bishop 1986a).

Collecting in the Carlile Shale *Linuparus* Assemblage Zone (Bishop & Williams 1986), yielded a single crab (Figs. 1, 2) not assignable to any existing species. This specimen is herein described and named *Homolopsis williamsi.*

A second new species of *Homolopsis* (Figs. 3, 4) was discovered in the lower Pierre Shale while collecting with Austin B. Williams on the Heart Tail Ranch during the summer of

1989. This specimen was immediately recognized as a *Homolopsis* because of the typical, well differentiated carapace with tumid lobes surmounted by a typical complement of boss-like spines. This specimen was collected from the Heart Tail Ranch Assemblage (Bishop 1985, 1987), which is also a decapod-rich, apatite-preserved decapod-worm association (Bishop 1987). This fauna consists of eight decapod species associated with ubiquitous worm burrows and fecal pellets, abundant baculitid cephalopods, scarce rudistid mollusks (*Titanosarcolites*), thin-shelled oysters (*Ostrea*), gastropods (*Trachytriton* and *Graphidula*), and abundant trace fossils. The decapod portion of the fauna, which now consists of 1644 specimens, is dominated by the decapods *Protocallianassa russelli* Bishop, 1985 (74.0%), *Necrocarcinus davisi* Bishop, 1985 (14.6%), and *Hoploparia mickelsoni* Bishop, 1985 (9.5%) but includes also *Raninella oaheensis* Bishop, 1978, *Dioratiopus hearttailensis* Bishop, 1985, *Xanthosia occidentailis* Bishop, 1985 (Bishop 1991), *Rugafarius fredrichi* Bishop, 1985, *Dromiopsis kimberlyae* Bishop, 1987, and *Homolopsis centurialis* new species. The low rate of incidence of *H. centurialis* in the Heart Tail Ranch Assemblage (1 specimen in 1644) indicates the probability of finding additional specimens is very small. The description of *H. williamsi* and *H. centurialis* expands the North American record for *Homolopsis*, and facilitates the review of the stratigraphic and paleogeographic distribution of this genus.

Type specimens of the new species are deposited in the collection of the Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota 57701.

Systematic Paleontology

Subsection Archaeobrachyura Guinot, 1977

Family Holmolidae Bell, 1863

Genus *Homolopsis* Bell, 1863

Type species.—*Homolopsis edwardsi* Bell, 1863, from the Albian of Folkstone, Kent.

Diagnosis.—Carapace more or less rectangular, ranging from much longer than wide to slightly wider than long, flat to moderately arched, lobes often tumid; moderately to highly sculptured with prominent, transverse, cervical and oblique branchiocardiac grooves passing anterior of epigastric lobes which usually form widest part of carapace. Orbital margins long, diverging backward, orbits subquadrate. Lateral margins parallel to slightly convergent posteriorly. Posterior margin straight to concave, often bordered by thin, raised rim. Rostrum triangular, downturned. Orbital regions open, eyestalk resting against hepatic lobe. Legs long, narrow, spinous. Chelipeds subequal, robust, often ornamented with longitudinal ridges and tubercles.

Discussion.—*Homolopsis* is known (see Fig. 6) from the Early Cretaceous of Europe and Australia, being found in the Neocomian of France (*Homolopsis tuberculata* Van Straelen 1936). *Pithonoton planum* Van Straelen, 1936, from the Neocomian of France, was reassigned to *Homolopsis* and *Prosopon schneideri* Stolley, 1924, from northern Germany, was questionably assigned to *Homolopsis* by Wright & Collins (1972). *Homolopsis* occurs in the Albian and Cenomanian of Great Britain (*H. glabra* Wright & Collins, 1972, *H. brightoni* Wright & Collins, 1972, and *H. edwardsi* Bell, 1863). *Homolopsis* is known from the Late Cretaceous of northern Germany and Scandinavia in the lowest Senonian (*H. gibbosa* Schlüter, 1868), the upper lower Senonian (*H. schlueteri* Beurlen, 1928), and from the Maastrichtian and Danian (*H. transiens* Segerberg, 1900). In North America, *Homolopsis* is known from the Late Cretaceous on the northern Atlantic Coastal Plain in the mid-early Campanian (*H. atlantica* Roberts, 1962 and *H. dispar* Roberts, 1962) and from the Western Interior Seaway from the Turonian (*H. williamsi*, new species), mid-early Campanian (*Homolopsis centurialis*, new species), and the Maastrichtian (*H. punctata* Rathbun, 1917).

Two problematic species have been described from Australia: *H. etheridgei* (Woodward, 1892) which probably is better assigned to *Zygastrocarcinus* Bishop, 1983 and *Homolopsis spinulosa* Glaessner, 1980, which, although clearly a homolid, is sufficiently different morphologically to warrant eventual assignment to a new genus.

Homolopsis williamsi, new species
Figs. 1, 2, 5a

Diagnosis.—Carapace rectangular, longer than wide, flat, deeply grooved with prominent cervical and branchiocardiac grooves. Lateral margins convergent posteriorly, posterolateral margins strongly tuberculate. Regions smooth, non-tumid.

Types.—Holotype, SDSM 11,014.

Occurrence and preservation.—The specimen of *H. williamsi* was collected on land belonging to Norman Durr in the SE ¼, NE ¼, section 15, T. 9 N, R. 2 E, Butte County, South Dakota. The dorsal surface of the specimen, preserved as an internal steinkern enclosed in an apatite concretion along with several plates of prisms of the bivalve mollusk *Inoceramus*, is crushed slightly downward into the visceral cavity. Cross sections of some appendages are visible on the exterior surface of the concretion, and the dorsum of the steinkern is slightly corroded and therefore does not exhibit traces of the external ornamentation of the carapace.

Description.—Carapace rectangular, longer (13.42 mm) than wide (12.53 mm), widest at anterolateral processes approximately ¼ distance from front. Anterolateral margins oblique, long; lateral margins somewhat convergent posteriorly, slightly curved; posterolateral edge fairly angular, ornamented by 4–5 large tubercles anteriorly; posterior margin concave. Dorsum flat, regions (as defined by Wright & Collins 1972:fig. 1) well delineated by deep, distinct grooves. Cervical groove deeply incised from gastric ridge nearly to edge of dorsum, faintly visible across gastric ridge separating dorsum into anterior portion (cephalic arch of Milne-Edwards as defined by Bell 1858:iii) and posterior portion (scapular arch of Milne-Edwards as defined by Bell 1858:iii). Groove delineating mesogastric region deep and well defined, sweeping backward and outward, crossing cervical groove and extending onto mesobranchial lobe before looping inward along posterior margin of urogastric lobe and anterolateral margin of cardiac lobe (forming the epimeral peninsulas), then joining brachiocardiac furrow and sweeping outward and forward to dorsal edge. A fainter groove branches off proximal branchiocardiac groove to delineate posterolateral edges of cardiac lobe which is separated by a shallow transverse furrow from intestinal lobe. Anteriorly, faint grooves separate protogastric and hepatic lobes. Protogastric lobe separated by very faint groove into narrow proximal area and larger distal area surmounted by tiny tubercles. Hepatic lobe consists of large proximal area separated by faint groove from smaller distal area inflated into a small boss surmounted by single tiny tubercle. Mesogastric lobe has a long, narrow anterior tongue extending onto rostral area apparently downturned into bifurcated rostrum, and abruptly widens posteriorly into triangular mesogastric lobe which, being weakly separated from urogastric lobes, forms a rather urn-shaped combined area.

Scapular arch well delimited by deep furrows into gastric ridge and branchial lobes. Gastric ridge barely differentiated by cervical furrow between mesogastric and urogastric lobes but well delimited by branchiocardiac groove laterally. Cardiac and intestinal lobes more or less fused and nearly separated from urogastric lobe by deep groove. Branchial region differentiated into large, posterior metabranchial lobe and smaller, anterior mesobranchial-epibranchial lobe. Mesobranchial lobe faintly separated from distal epibranchial lobe by very shallow groove splitting off cervical groove. Epibranchial lobe inflated and angular, forming epibranchial angle and widest portion of carapace accentuated by curvature

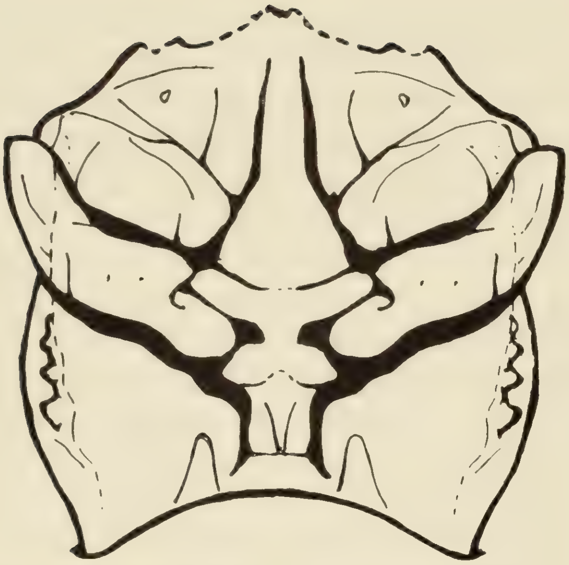

Fig. 1. Reconstruction of carapace of *Homolopsis williamsi,* new species, dorsal view.

of cervical furrow around inner and anterior margin of epibranchial lobe. Two tiny marginal tubercles on dorsal edge of the epibranchial lobe in line with tubercles on posterolateral margin. Mesobranchial lobe somewhat separated into proximal and distal areas by shallow groove which is posterior extension of cervical furrow near lateral edge of urogastric lobe. Metabranchial lobe mostly flat but with subtle ridge proximally, and 4 marginal tubercles just posterior to intersection of branchiocardiac furrow and dorsal edge.

Carapace crushed along linea homolica which lies just inside dorsal shield lateral margins, extending from posterior margin to just outside orbits, slightly arcuate inward.

Etymology.—This species is named in honor of my colleague and friend, Austin B. Williams, who has dedicated so much of his professional life to the study of the decapod crustaceans.

Comparison.—*Homolopsis williamsi* is easily distinguished from its North American congenors *Homolopsis centurialis* n. sp. (Fig. 5b), *H. atlantica* (Fig. 5d), *H. dispar* (Fig. 5e), and *H. punctata* (Fig. 5c), and nearly all other homolopsids because of its lack of tumid lobes and lack of boss-like ornamentations which are characteristic of

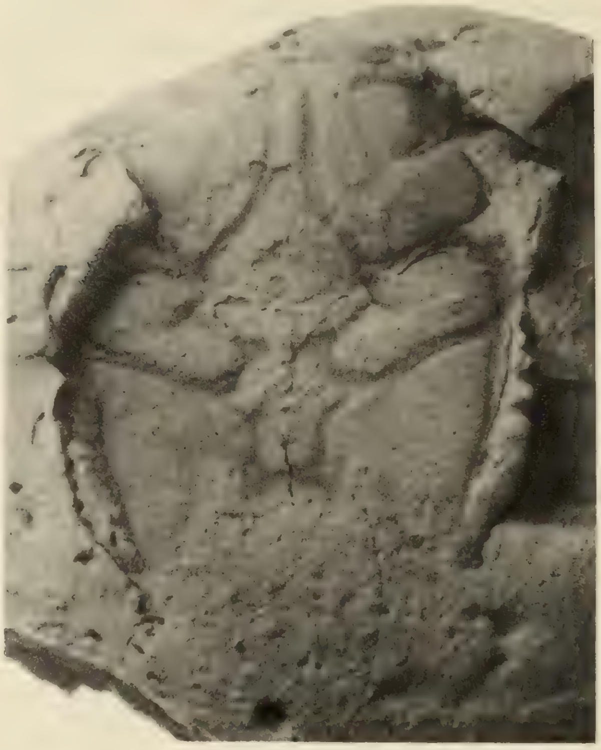

Fig. 2. Photograph of holotype of *Homolopsis williamsi,* new species, dorsal view, embedded in apatite concretion. (Scale = 1 cm)

virtually every other species of *Homolopsis* except for *H. glabra. Homolopsis williamsi* most resembles *H. glabra* from which it is distinguished by being more rectangular and relatively longer, by lacking the well-defined medial part of the cervical groove present in *H. glabra,* by lacking the well-defined distal epibranchial furrow present in *H. glabra,* and by possessing large tubercles on the posterolateral margin lacking in *H. glabra.*

Remarks.—The presence of *H. williamsi* in the *Linuparus* association from the Carlile Shale reemphasizes the need for large collections of decapods from apatite-preserved decapod-rich assemblages. Only collections numbering in the hundreds or thousands are likely to to have a significant chance of yielding scarcer faunal elements such as *H. williamsi.*

The preservation of a steinkern such as the holotype of *H. williamsi,* does not present a complete complement of morphologic information particularly on the exterior of the cuticle; however, the gross morphology preserved is adequate to define this new taxon. The complete description of this crab's morphology must await a time when another specimen is found with preserved exoskeleton and appendages. Because this is a minor taxon in the *Linuparus* association (abundance of 0.06%), it is anticipated that another thousand specimens will have to be collected before we can find another specimen of *H. williamsi.* The breakage of the specimen parallel to the edges of the dorsal shield margins along the linea homolica is typical of the homolopsid crabs.

Homolopsis centurialis, new species
Figs. 3, 4, 5b

Diagnosis.—Carapace more or less rectangular, longer than wide, moderately arched, with oblique cervical and branchiocardiac grooves; lobes moderately tumid, moderately sculptured. Lateral margins parallel, slightly convergent posteriorly; posterior margin concave and sinuous. Rostrum triangular, downturned; orbital regions unknown. Anterior protogastric boss most distal; posterior medial metagastric boss small and posteriorly situated; cardiac region inflated, finely granulate, and transverse.

Types.—Holotype, SDSM 11,015.

Occurrence and preservation.—The specimen of *H. centurialis* was collected on the Heart Tail Ranch in the NW ¼, SE ¼, NE ¼ section 17, T. 11 N, R. 2 E, Butte County, South Dakota. The specimen, preserved in an apatite concretion, is crushed slightly and broken along the linea homolica with the carapace sides splayed outward into the plane of the carapace dorsum. External ornamentation is preserved on the cuticle.

Description.—Carapace rectangular, longer (13.9 mm) than wide (13.5 mm), widest at anterolateral processes approximately ⅓ length from front. Anterolateral margins oblique, long; lateral margins convergent posteriorly, nearly straight; posterolateral edge fairly angular, ornamented by 4 small tubercles; posterior margin concave, sinuous. Dorsum slightly arched, regions (as defined by Wright & Collins 1972:fig. 1) well delineated by moderately deep, distinct grooves. Cervical groove present from gastric ridge nearly to edge of dorsum, faintly visible across gastric ridge separating dorsum into an anterior portion (cephalic arch of Milne-Edwards as defined by Bell 1858: iii) and posterior portion (scapular arch of Milne-Edwards as defined by Bell 1858:iii). Branchiocardiac groove incomplete, beginning at its junction with mesogastric groove, crossing cervical groove and sweeping backward and inward behind urogastric lobe, then turning outward and sweeping forward from behind epimeral peninsula, separating mesobranchial-epibranchial lobes and sweeping outward and forward to dorsal edge. Groove separating mesogastric from urogastric lobe indistinct on gastric ridge but continued onto epigastric lobe as better defined groove. Transverse shallow depression forms posterior edge of cardiac region separating it from intestinal lobe. Anteriorly a faint groove separates protogastric and hepatic lobes. Protogastric lobe surmounted by 3 moderately-sized and 1 tiny boss situated at anterodistal, proximomedial, posterodistal, and posterior parts of protogastric lobe. Hepatic lobe carries two marginal lobes separated by shallow depression. Mesogastric lobe has long, narrow anterior tongue which extends onto rostral area, apparently downturned into triangular rostrum and widens around anterior boss situated near anterior protogastric bosses to form a more or less continuous U-shaped arc with them; anterior process then narrows slightly but abruptly widens around base of triangular mesogastric lobe.

Scapular arch poorly delimited by shallow furrows. Gastric ridge barely differentiated by cervical furrow between mesogastric and urogastric lobes but better delimited by transverse extension of branchiocardiac groove behind urogastric lobe separating it from cardiac and intestinal lobes poorly dif-

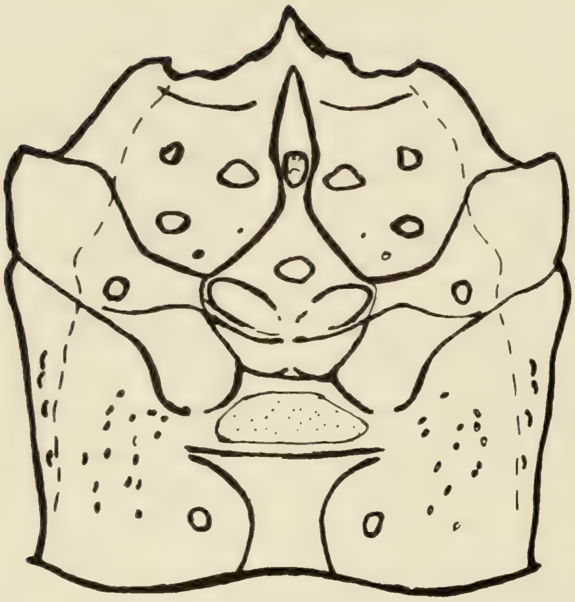

Fig. 3. Reconstruction of carapace of *Homolopsis centurialis,* new species, dorsal view.

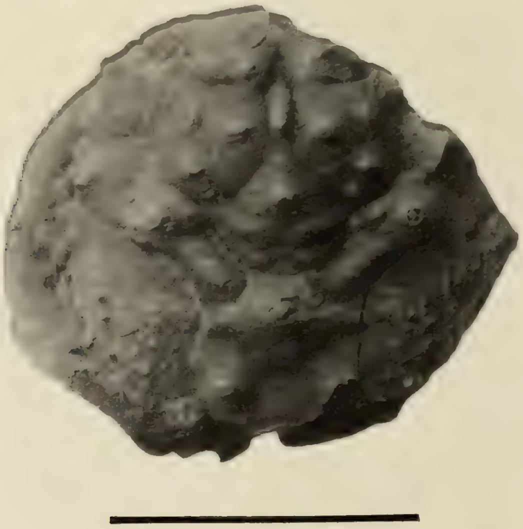

Fig. 4. Photograph of holotype of *Homolopsis centurialis,* new species, dorsal view, embedded in apatite concretion with sides of carapace splayed outward into plane of dorsum. (Scale = 1 cm)

ferentiated one from another. Branchial region differentiated into large, posterior metabranchial and mesobranchial lobe and well differentiated anterior epibranchial lobe. Mesobranchial lobe separated from epibranchial lobe by shallow groove. Epibranchial lobe inflated and ridge-like, forming epibranchial angle and widest portion of carapace, accentuated by curvature of cervical furrow around inner and anterior margin of epibranchial lobe. Two boss-like tubercles present on epibranchial lobe, one on dorsum and one on vertical wall of carapace. Metabranchial lobe arched with subtle ridge proximally carrying small boss and with 4 small marginal tubercles near middle; surface ornamented by coarse tuberculation. Carapace sides splayed outward along the linea homolica, leading to a misrepresentation of the dorsal morphology of this species which is idealized in Fig. 3.

Etymology.—Trivial name of binomen is taken from the Latin "centurialis," meaning "of a hundred" in honor of its discovery during South Dakota's centennial celebration.

Comparison.—*Homolopsis centurialis* is a typical homolopsid crab exhibiting most characteristics of the genus, including tumid areolations, boss-like projections on most lobes, and granulation over much of the carapace, all characteristics which easily distinguish *H. centurialis* from *H. williamsi* (Fig. 5a) and *H. glabra. Homolopsis centurialis* is most similar to *H. punctata* (Fig. 5c), from which it can be distinguished by its significantly different pattern of protogastric bosses in which the two anterodistal bosses are on a line parallel to the sagittal axis rather than on a line steeply inclined to the sagittal axis as in *H. punctata,* by having a differently-shaped cardiac region which is transverse and relatively short rather than diamond-shaped as in *H. punctata,* and by having relatively more poorly developed bosses than in *H. punctata. Homolopsis centurialis* is similar to *H. dispar* (Fig. 5e) in possessing relatively poorly developed bosses, but differs from that species by having a more poorly defined cervical groove on the sagittal ridge, being more granulate, by having a better developed boss on the anterior process of the mesogastric lobe, by having a significantly better developed boss on the proximal part of the epigastric lobe, and by lacking the well-developed epigastric bosses. *Homolopsis*

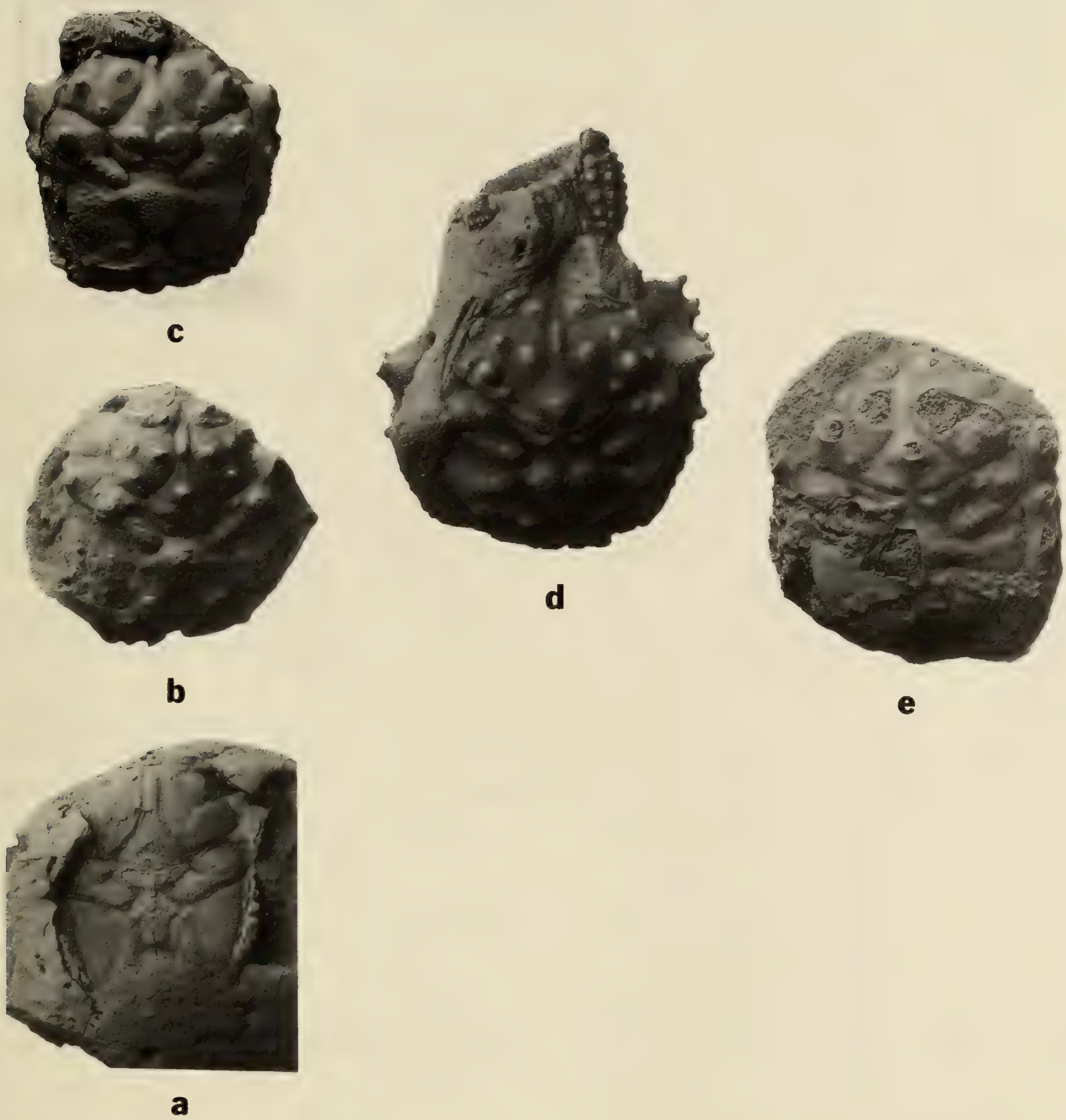

Fig. 5. North American species of *Homolopsis* Bell, 1863, arranged in stratigraphic sequence and approximate geographic position (left toward west, right toward east): Western Interior species; a, *Homolopsis williamsi,* new species; b, *H. centurialis,* new species; c, *H. punctata,* Rathbun, 1917; and Northern Atlantic Coastal Plain species; d, *H. atlantica,* Roberts, 1962; e, *H. dispar,* Roberts, 1962.

centurialis differs significantly from *H. atlantica* (Fig. 5d) by its less well-developed bosses, less tumid lobes, a more subdued anterolateral margin perhaps lacking the prominent anterolateral hepatic spines, by having four well developed protogastric bosses rather than the six, a continuous transverse cardiac lobe rather than the transversely-bilobed cardiac region, and the lack of a transverse metabranchial ridge.

Homolopsis centurialis is similar to *H. brightoni* from which it is distinguished by being relatively longer, having a poorly differentiated protogastric lobe, and transversely-ridged cardiac lobe (rather than the diamond-shaped cardiac lobe of *H. brightoni*). *Homolopsis centurialis* differs significantly from *H. edwardsi* by being rectangular rather than oval, the small epibranchial spines, less developed posterolateral spination, and numerous differences in placement of the coarse ornamentation on the various lobes (see also Carter 1898:21–22). *Homolopsis centurialis* differs from *H. tuberculata* Van Straelen, 1936 by having relatively reduced ornamentation, possessing a boss on the anterior process of the mesogastric lobe (lacking in *H. tuberculata*), and having a different pattern of protogastric bosses. *Homolopsis centurialis* differs from *H. schlueteri* (Beurlen, 1928 by being significantly shorter, by possessing a very different pattern of bosses, and by having differently shaped mesogastric and cardiac lobes. *Homolopsis centurialis* differs from *H. transiens* Segerberg, 1900 by possessing medial bosses on the mesogastric lobe lacking in *H. transiens,* by having a less developed cervical furrow across the gastric ridge, and a different distribution of bosses on the protogastric lobe. *Homolopsis centurialis* differs from *H. gibbosa* (also see Mertin 1941:230, fig. 25) by its posteriorly converging shape where *H. gibbosa* converges anteriorly, by having 4 protogastric bosses where *H. gibbosa* has 5 arranged in a different pattern, and by lacking the bilaterally arranged cardiac bosses of *H. gibbosa.*

Homolopsis centurialis differs from *Pithonoton planum* Van Straelen, 1936, and from *Prosopon schneideri* Stolley, 1924, by having a typically well-developed homolopsid morphology rather than prosoponid, although, as pointed out by Wright & Collins (1972:45), *P. planum* appears to be very close to the ancestral line leading to the homolopsids.

Paleogeography and Biostratigraphy of *Homolopsis*

The species assignable to the genus *Homolopsis* show an interesting pattern of development and evolution (Figs. 6, 7) indicating an origin in the northern Tethys Seaway in the Neocomian (Early Cretaceous) possibly from prosoponid ancestors. Glaessner (1969:R490) briefly summarized the systematics of the Homolidae and provided an illustration of a possible Jurassic ancestor, ?*Titanohomola,* Glaessner, 1933. Wright & Collins (1972:45) suggested that *Pithonoton planum* Van Straelen (1936:27, Pl. 4, fig. 1) and *Prosopon schneideri* Stolley (1924:413, Pl. 13, fig. 1) were close to ancestral forms for *Homolopsis* and, particularly, *P. planum* was cited as a possible "young specimen of an ancestral *Homolopsis,* distinguished from *H. glabra* mainly by the stronger median furrow on the urogastric lobe and stronger cardiac tubercles." Although I have not seen the specimens representing *P. planum,* Van Straelen's figures (1936:Pl. 4, figs. 1, 2) certainly force me to concur with Wright & Collins. Three distinct lineages of homolid crabs were derived from the early ancestors of the homolids by the Albian; those assignable to *Homolopsis,* to *Zygastrocarcinus* Bishop 1983, and the aberrant Australian species *Homolopsis*? *spinulosa.* The species of *Homolopsis* migrated and evolved in the shallow waters of the northern Tethys in northern Europe (*H. gibbosa, H. schneideri,* and *H. transiens*), the Northern Atlantic Coastal Plain (*H. atlantica* and *H. dispar*), and in the Western Interior of the USA (*H. williamsi, H. centurialis,* and *H. punctata*) (Bishop, 1986b). Members of the genus *Zygastrocarcinus* [*Z. etheridgei* (H. Woodward, 1892); *Z. mendryki* (Bishop, 1982); *Z. griesi* Bishop, 1983; *Z. richardsoni* (Woodward, 1896); *Z. japonica* Yokoyama, 1911; and *Z. gorrelli* (Rathbun, 1926], have a more western Tethys (i.e., Tethyan-Pacific) distribution overlapping that of *Homolopsis* in the Western Interior Seaway. *Homolopsis*? *spinulosa* from the Upper Cenomanian of Australia probably represents a third lineage of Cretaceous homolid evolution, one which apparently went rapidly to extinction.

The pattern of evolution of *Homolopsis* s.s. is one of initial development in the Neocomian in Central and Northern Europe, emigration and adaptive radiation in the shallow waters of southern England, followed by emigration and speciation in

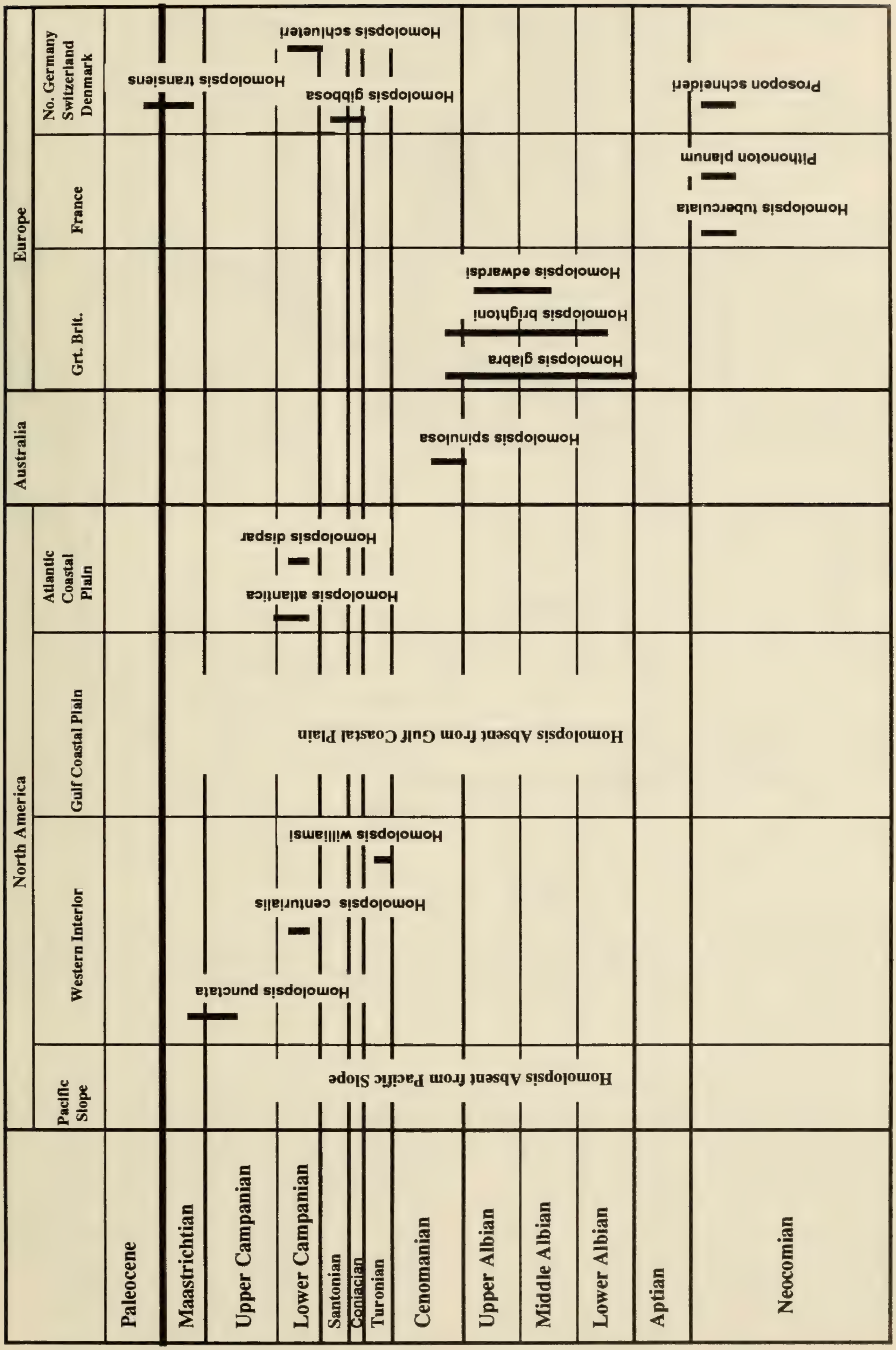

Fig. 6. Stratigraphic range chart showing ranges and biogeographic positions of species of *Homolopsis*, Bell, 1863, and closely related prosoponids.

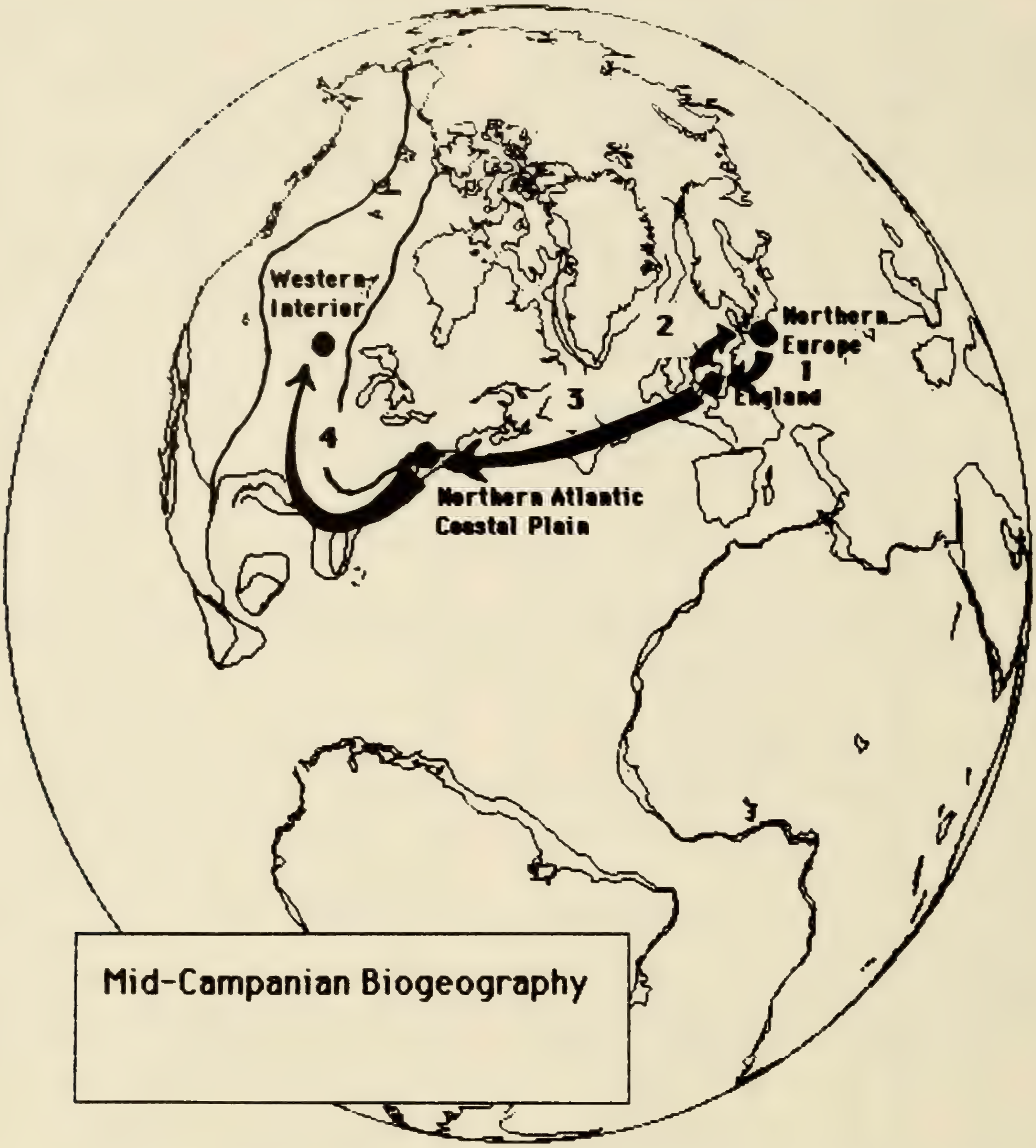

Fig. 7. Late Cretaceous paleogeography illustrating the wave-like pattern of emigrations of *Homolopsis,* Bell, 1863, from Central Europe into Great Britain (Southern England) (1) and subsequently into Northern Europe (2), the Northern Atlantic Coastal Plain of the United States (3), and the Western Interior Seaway of the United States (4).

Northern Europe, the Northern Atlantic Coastal Plain, and the Western Interior Seaway. Only *H. transiens* is known to have survived the mass extinctions at the Cretaceous-Tertiary boundary. No other record of Cenozoic species of *Homolopsis* is known.

The modern homolids *Homola* and *Latreillia* are deep-water forms. The carapace similarity between the typical fossil species of *Homolopsis* and the Recent *Homola barbata* (Fabricius, 1793) is truly remarkable, strongly suggesting that *Homola* is a direct descendent of one of the Cretaceous species of *Homolopsis.* This pattern of retreat into deep water refugia is seen in other decapod taxa (e.g., linuparid lobsters, retroplumid crabs) and would account for the sparse record of Cenozoic forms because of the relative lack of preservation of deep water sediments in the geologic record.

Acknowledgments

I extend sincere thanks to Chance and Cindy Davis for granting permission to collect on the Heart Tail Ranch and to Norman Durr for permission to collect on his land north of Belle Fourche. Special acknowledgment is made to all those assisting me in the field and helping slowly build the collection upon which this research is based. Direct support for this research has been received from the Committee for Research and Exploration, National Geographic Society, the Faculty Research Committee, Georgia Southern University, and the Museum of Geology, South Dakota School of Mines. Rodney Feldmann read the original manuscript and strengthened it with his suggestions.

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MIOCENE FOSSILS OF THE GENUS *CANCER* (DECAPODA: CANCRIDAE) FROM NORTHWESTERN WASHINGTON, U.S.A.

James L. Goedert and Ross E. Berglund

Abstract.—Recently collected fossil crab cheliped parts from the late middle Miocene age Quillayute Formation in northwestern Washington are the geochronologically oldest record of the extant cancrid crab *Cancer magister,* and the northernmost record for the extinct *Cancer coosensis.*

The extant "Dungeness crab," *Cancer magister* Dana, 1852, inhabits shallow waters of the Northeast Pacific Ocean from Unalaska, Alaska to Monterey, California (Nations 1975). Fossils referable to *C. magister* were identified by Nations (1975) from Pleistocene and Pliocene age rocks in Oregon and California. A crab with chelipeds similar to those of *C. magister,* from middle Miocene to lower Pleistocene rocks of Oregon and California, was named *Cancer coosensis* by Nations (1975).

Some of the specimens discussed by Nations (1975) were collected from the Coos Conglomerate Member of the Empire Formation, near Coos Bay, Oregon. These were thought to be of early Pliocene age, but the Coos Conglomerate Member is now considered to be latest Miocene (Armentrout et al. 1983).

Collections of fossils from a single outcrop of the Quillayute Formation in northwestern Washington now extend the geochronologic record of *Cancer magister* back to late middle Miocene time, and extend the geographic range of *C. coosensis* northward into Washington. The Quillayute Formation is known from only a few outcrops along the Bogachiel River and the Soleduck (Solduc) River (Tabor & Cady 1978, Rau 1979) in Clallam County, Washington, and consists of massive sandstone containing mollusk-rich conglomerate in channel deposits. The fossil mollusks are correlative with the Wishkahan Provincial Molluscan Stage (Addicott 1976:107) which is late middle Miocene in age (Armentrout et al. 1983).

The crab fossils from the Quillayute Formation are deposited in the collections of the Thomas Burke Memorial Washington State Museum, University of Washington, Seattle (UWBM). They were collected from a mollusk-rich channel deposit at locality UWBM B5551, a bluff on the south side of the Bogachiel River, just west of the mouth of Maxfield Creek, Clallam County, Washington. Detailed locality information is available upon application to UWBM.

Systematic Paleontology

Family Cancridae Latreille, 1803
Subfamily Cancrinae Latreille, 1803
Genus *Cancer* Linnaeus, 1758
Cancer magister Dana, 1852
Fig. 1

Referred material.—Right propodus, UWBM 66001, collected by J. L. Goedert, 19 Aug 1989.

Remarks.—The general morphology of UWBM 66001 is typical of the genus *Cancer,* and closely resembles the mani of *C. magister, C. durhami* Nations, 1975, and *C. coosensis* Nations, 1975. Because of the fragmentary preservation of UWBM 66001, comparisons with these three species is lim-

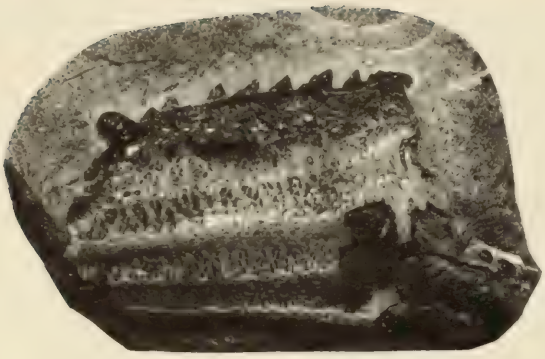

Fig. 1. *Cancer magister.* Outer view of right manus, UWBM 66001, ×0.8, collected from the Quillayute Formation in northwest Washington.

ited to decorative features and ratios of cheliped measurements (see Nations 1975).

As in *Cancer magister, C. durhami,* and *C. coosensis,* the propodus is robust, the outer surface of the manus is carinate, with the first carina (upper margin) typically spinous. Granules in spaces between the lower four carinae of UWBM 66001 roughly align transversely (vertically). This alignment of granules was noted by Nations (1975) on specimens of *C. magister,* but not on *C. durhami* or *C. coosensis.*

As on the inner surface of the mani of *Cancer magister, C. durhami,* and *C. coosensis,* the upper half of UWBM 66001 is nearly free of granulation. On the lower half of the inner surface of UWBM 66001, two irregular bands of granules that correspond, approximately, to carinae 4 and 5 on the outer surface, extend longitudinally the full length of the manus. Similar bands of granules were noted by Nations (1975) for *C. magister, C. durhami,* and *C. coosensis.*

Cheliped measurement ratios for UWBM 66001 compare very closely to those of *Cancer magister,* and differ greatly from those of *C. durhami* and *C. coosensis* given by Nations (1975). This specimen (UWBM 66001) is best referred to *Cancer magister* because of similar decorative granulation and comparative measurement data.

Measurements (mm).—Length, upper margin (Lu) 35.5; height of manus (Hm) 34.0; thickness of manus (Tm) 17.4; height, fixed finger (Hff) 13.0; thickness, fixed finger (Tff) 8.6. Cheliped ratios, Lu:Hm 1.044; Tm:Hm 0.512; Hff:Hm 0.382; Tff:Hff 0.661.

Cancer coosensis Nations, 1975

Referred material.—Moveable finger, UWBM 76312, collected by K. L. Kaler, 1990.

Remarks.—This specimen is too incomplete and abraded to provide informative measurements; however, the characters which are preserved have considerable resemblance to those on the moveable fingers of several species of *Cancer.* The spinous upper margin is most like those of *C. magister, C. durhami,* and *C. coosensis.* The evenly shaped and spaced spines of UWBM 76312 resemble those of *C. magister* and *C. durhami,* differing from *C. coosensis,* in which the spines are irregular in both shape and spacing. The outline of the finger is long and narrow, much like that of *C. magister* and *C. coosensis.*

The moveable fingers of *Cancer magister, C. durhami* and *C. coosensis* all bear seven cutting teeth, as does UWBM 76312. These teeth are proximally rounded and become smaller and more blade-like distally, most like those of *C. magister* and *C. coosensis.* Spacing between the teeth is wide, as in *C. coosensis,* not closely spaced as in *C. magister.* Subsidiary cusps, like those noted by Nations (1975) on some teeth of *C. durhami,* are not present on UWBM 76312.

The outer surface of UWBM 76312 resembles that of *C. magister,* being granulate proximally, and sparsely granulate toward the tip. This differs from *C. coosensis* which is coarsely granulate throughout. Two continuous rows of setiferous pits, dividing the outer surface into thirds with little discernable grooving, are present on UWBM 76312 and *C. coosensis,* but not on *C. magister* or *C. durhami.* On the inner surface of the moveable finger of *C. magister, C. durhami,* and *C. coosensis,* there is a shallow furrow along the median with rounded ridges above and below (Nations 1975), but only in *C.*

coosensis are both ridges completely covered with granules as in UWBM 76312. The tip of UWBM 76312 is darkened, as is typical of *C. coosensis.*

Although UWBM 76312 shares some characters with *Cancer magister* and *C. durhami,* it bears closest resemblance to *C. coosensis,* to which it is tentatively referred until better and more complete material becomes available.

Acknowledgments

We thank J. Putnam for photographs and K. L. Kaler for donating specimens, G. H. Goedert for assisting in the field, and F. Kaler for several helpful suggestions. We also thank J. D. Nations and A. B. Williams for helpful reviews.

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A NEW CRAWFISH OF THE GENUS *ORCONECTES* FROM THE YAZOO RIVER SYSTEM OF MISSISSIPPI (DECAPODA: CAMBARIDAE)

J. F. Fitzpatrick, Jr. and Royal D. Suttkus

Abstract.—The crawfish *Orconectes* (*Hespericambarus*) *hartfieldi*, is described from five sites in the Yazoo River system of Mississippi. It is distinguished by a notch near the apex of the central projection of the first pleopod of the first form male, and the annulus ventralis of the female is the most sculptured in the subgenus. Its closest relatives seem to be *O.* (*H.*) *hathawayi* Penn and *O.* (*H.*) *perfectus* Walls; geographically, it is distributed between the ranges of the two.

Most of the populations of members of the crawfish genus *Orconectes* that occur in the Big Black, Tombigbee, and Yazoo systems of Mississippi currently are not assigned trivial names. Most of them, nevertheless, can be relegated to the subgenus *Gremicambarus* (Fitzpatrick, 1987), but otherwise they are so similar in morphology that it is difficult to separate one interbreeding group from another. This was recognized by Cooper & Hobbs (1980:1) when they observed: "Unfortunately, without first form males, we have been unable to identify specimens in the genus from many localities in the Mobile and Tennessee basins." They emphasized the need for knowledge of the precise limits of variation in the non-secondary sexual characters. Otherwise, only the morphology of the first pleopod of Form I males is reliable for the identification of species. We can add that even the character states of non-sexual features, without good series for comparison, can be misleading. We can likewise include the Big Black and Yazoo basins in systems inhabited by such populations.

When Walls (1972) described *Orconectes* (*Hespericambarus*) *perfectus*, he implied that similar situations exist in this subgenus. Although morphologically similar populations occur throughout the Tombigbee basin and many were at his disposal, he expressly limited his paratypic series to a few populations in the immediate vicinity of the type locality. Recently, one of us (RDS) collected first form males and other specimens assignable to this subgenus from four widely spaced localities in the Yazoo basin. The first pleopod of the Form I male and the annulus ventralis of the female are sufficiently distinctive that we are secure in our belief that these populations represent a previously undescribed species. Further, the geographic dispersal, enhanced by another single Form I male collected in 1967 from yet another distant locality, precludes the possibility that the specimens are local or abnormal variants.

Orconectes (*Hespericambarus*) *hartfieldi*, new species
Fig. 1

Diagnosis.—Pigmented; eyes normal. Rostrum with slightly thickened, somewhat converging margins ending cephalically in small acute spines; lacking median carina; acumen distinct, moderately long, and clearly delimited basally from remainder of rostrum. Areola obliterated for most of length and comprising 31.9 to 35.2% (avg. 33.3%) of total carapace length, and 44.1 to 47.6% (avg. 45.7%) of postorbital carapace length. Cervical spine prominent; suborbital angle absent; postorbital ridge well developed and terminating cephalically in strong acute spine. Antennal scale usually 2.06 times longer than wide and widest slightly distal to midlength. Chelae of adult males inflated, slightly costate laterally at best, and covered by numerous setae occurring in loose tufts originating in shallow punctations; mesial margin with 3 to 7 small to moderate-sized acute spines or spiniform tubercles; tubercles extending onto basal half of mesial margin of dactyl in varying degrees of development and number, often with squamous or low spiniform tubercles flanking mesial row of spines above and below; opposable margins of both fingers with small tubercles in basal half and slightly irregular band of minute denticles in distal half; both fingers with weakly developed longitudinal ridges flanked by scant setose punctations above and below. Hook on ischium of third pereiopod only, not opposed by tubercle on corresponding basis; coxae of pereiopods lacking boss. First pleopod of first form male reaching coxae of third pereiopod when abdomen flexed, lacking shoulder on cephalic surface, terminating in two elements, both inclined caudodistally; central projection longer and with slight subapical notch or shallow depression caudodistally; mesial process non-corneous, only slightly curved, tapering smoothly to subacute apex and directed caudomesially at about 45° angle to main shaft of appendage. Annulus ventralis of female as figured. First pleopod present in female.

Holotypic male, Form I.—Body and eyes pigmented. Cephalothorax (Figs. 1b, l) subovate in section, abdomen narrower than carapace (10.1 and 11.2 mm), width of latter greater than depth at caudodorsal margin of cervical groove (11.2 and 10.5 mm). Areola obliterated for most of length with usual subtriangular cephalic part and weakly developed divergent margins in caudal fifth of thoracic portion of carapace; length 33.3% of total length of carapace (45.9% of postorbital length). Rostrum with margins little thickened, elevated, slightly convergent, and bearing small but acute spines at base of clearly delineated acumen, latter almost reaching distal end of antennular peduncle; upper surface slightly concave, lacking median carina, and only sparsely punctate except for row flanking elevated margins mesially. Subrostral ridge weak, disappearing in dorsal aspect before reaching base of rostrum. Postorbital ridge heavy, with dorsolateral and dorsomesial grooves, terminating cephalically in strong acute spine. Suborbital angle absent. Cervical spine single, strong, and acute; branchiostegal spine well developed. Carapace studded with shallow setose punctations developing into granulose tubercles ventrolaterally. Abdomen shorter than carapace (22.8 and 23.7 mm); pleura well developed and rounded ventrally except that of second abdominal segment, which subtruncate; cephalic section of telson with 2 spines in each caudolateral corner, more mesial ones movable. Proximal podomere of uropod with acute spine on mesial lobe only; mesial ramus with distinct but weakly developed dorsomedian keel terminating in small premarginal spine; lateral ramus likewise keeled.

Cephalic lobe of epistome (Fig. 1n) lacking cephalomedian projection and delimited basally by distinctly contracted base; margins elevated with distinct notch (?old injury) on left side; cephalic lobe excavate with prominent longitudinal median ridge rising (ventrally) as high as margins; main body with deep, pit-like fovea; epistomal zygoma broadly arched. Basal segment of antennule with small spine on ventral surface slightly distal to midlength. Antennae almost reaching caudal margin of fifth abdominal segment. Antennal scale (Fig. 1k) 2.24 times as long as broad with greatest width slightly distal to midlength; mesial border of lamella rounded but less than evenly so; apical spine strong and reaching just beyond distal margin of ultimate podomere of antennal peduncle.

Right chela (Fig. 1m) depressed, weakly costate laterally only along basal half of immovable finger, 2.1 times longer than broad; all surfaces pubescent. Mesial margin of palm with row of 4 spiniform tubercles, somewhat obscured by pubesence and 1 rounded tubercle proximally; 2 small tubercles on mesial margin of dactyl near base obscured by pubesence. Fingers not gaping. Opposable margin of fixed finger with row of 6 tubercles in basal half and band of crowded minute denticles extending distally from penultimate tubercle of group, denticles interrupted half way to tip of finger by another small tubercle; additional tubercles ventral to aforementioned dentition at base of finger and at base of distal fourth of finger; all tubercles and denticles obscured by pubesence. Opposable margin of dactyl with 4 subequal tubercles in basal half and band of crowded minute denticles extending to apex of finger, large tubercle ventral to row at base of finger; all tubercles and denticles obscured by pubesence. Carpus about 1.2 times longer than broad, with arched groove dorsally, latrer flanked mesially by few low tubercles and laterally by scarce, very shallow punctations; mesial surface with spikelike tubercle distal to midlength and broadly triangular one subdistally; ventral surface with spiniform tubercle in mesiodistal and laterodistal corners. Dorsal surface of merus with 2 stout spines distally; lateral and mesial surfaces with scarce, shallow punctations; lower lateral margin with row of 8 small tubercles terminating distally in prominent spiniform one; lower lateral margin with evenly spaced row of 3 spiniform tubercles in distal half. Basis, ischium, and coxa with margins entire. Ischium of only third pereiopod with simple strong hook (Fig. 1j), latter overreaching distal margin of corresponding basis but unopposed by tubercle.

First pleopods symmetrical, reaching coxae of third pereiopods when abdomen flexed. First pleopods (Fig. 1a, c, g–i) as described in "Diagnosis"; subterminal excavation of central projection shallow, not distinct notch.

Allotypic female.—Differing from holotype, except in secondary sexual characteristics, in following respects: abdomen longer than carapace (31.0 and 28.1 mm) and only slightly narrower than carapace (12.8 and 13.0 mm). Mesial margin of palm with 5 spinose tubercles; distalmost tubercles of mesial margin of carpus much more spinelike and acute than others; lower lateral margin of merus with 4 tubercles and distally one low spiniform tubercle followed by ultimate strong spiniform tubercle.

Annulus ventralis (Fig. 1e) as illustrated; sinus originating lateral to midline in deep posteromesially inclined sulcus in cephalic third of annulus, continuing across midline before turning caudally to anterior border of caudal third of annulus, there turning sharply to midline and thence recurving to follow gently sinuous path to caudal margin. Postannular sclerite about half as wide as annulus and just over three times as broad as long. First pleopods small but distinct.

Morphotypic male, Form II.—Differing from holotype in following respects: mesial margin of palm with row of 3 low tubercles; mesial margin of carpus more like allotype than holotype; conspicuous gap between ultimate and penultimate spiniform tubercles of lower mesial margin of merus, lower lateral margin with row of 7 low tubercles proximally and distalmost two spiniform similar to those of allotype. Hook on ischium of third pereiopod weakly developed, not overreaching distal margin of corresponding basis. Cephalic lobe of epistome weakly excavate, lacking median longitudinal ridge; fovea of main body corresponding more shallow.

Color.—Color notes are available for the Panola County specimen. Base color olive tan diffused with darker brown and blue-black pigments. Rostral margins light; large irregular tan spot just posterior to caudal extremity of postorbital ridge. Density of dark pigment increasing dorsally so that

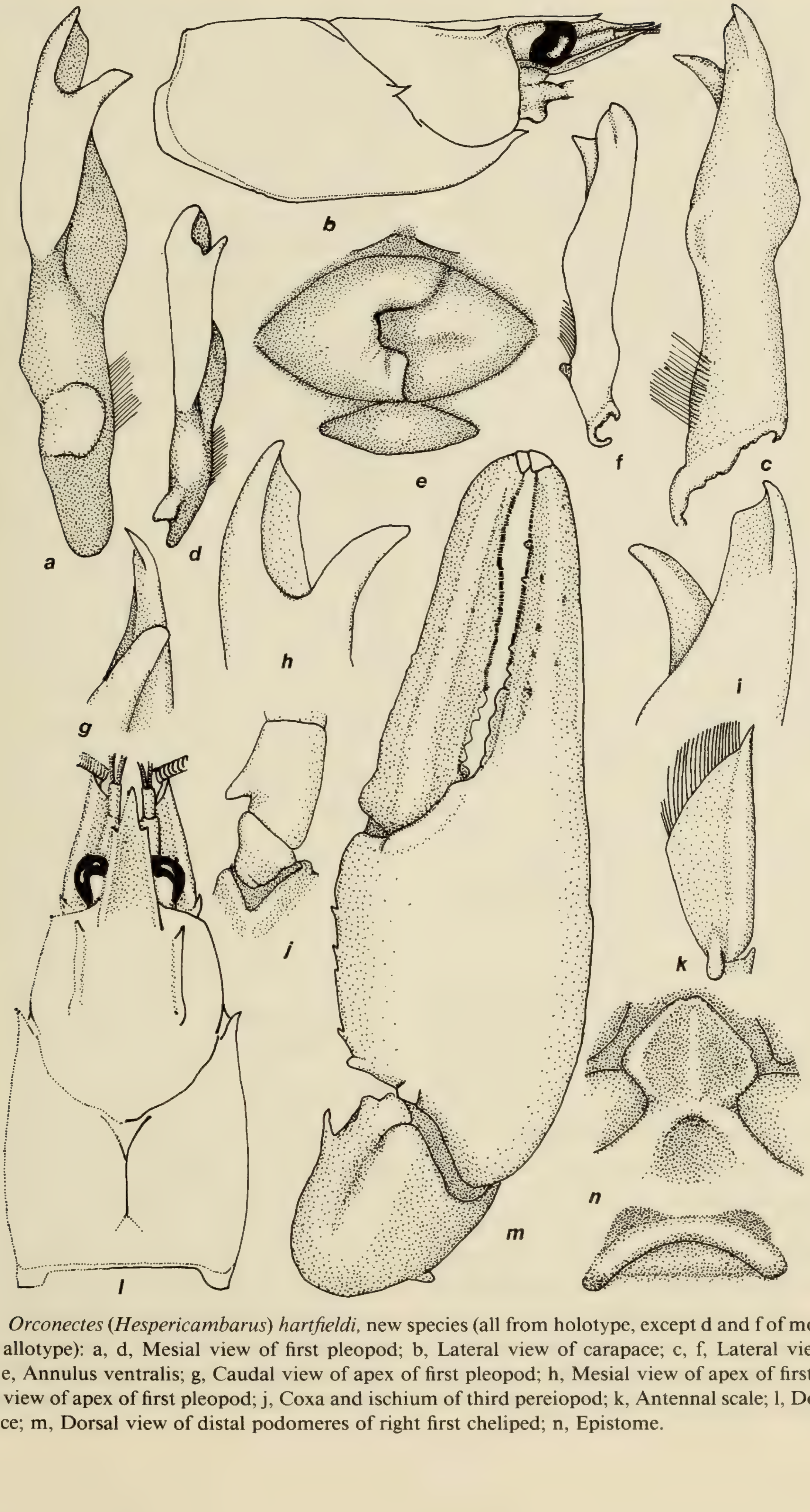

Fig. 1. *Orconectes* (*Hespericambarus*) *hartfieldi*, new species (all from holotype, except d and f of morphotype and e of allotype): a, d, Mesial view of first pleopod; b, Lateral view of carapace; c, f, Lateral view of first pleopod; e, Annulus ventralis; g, Caudal view of apex of first pleopod; h, Mesial view of apex of first pleopod; i, Lateral view of apex of first pleopod; j, Coxa and ischium of third pereiopod; k, Antennal scale; l, Dorsal view of carapace; m, Dorsal view of distal podomeres of right first cheliped; n, Epistome.

ventral half of carapace to about level of cervical spine pale tan, but dorsal half dark brown mottled with small light tan spots. Caudodorsal part of thoracic region posterior to cervical spines lighter with transverse rows of fine dark spots giving appearance of 4 stripes. Cephalic triangular area of areola nearly filled with blue-black subtriangular spot; irregularly shaped blue-black spot just above cervical spine and anterior to cervical groove; several large blue-black spots at dorsal caudolateral margin of carapace coalescing into large irregular patch just lateral to posterior flare of areola. Two undulant stripes running longitudinally along lateral faces of abdomen such that each segment provided with 2 chevrons, lower at junction of pleuron and tergum darker and thinner; pleurons and area between chevrons with numerous dark spots of varying size but always small; middorsal part of terminal segment similarly spotted but spots more dense and more regular in size and shape. Telson with thin blue-black line along lateral margin of cephalic portion, stripe expanding to encompass entire area of caudolateral spines; caudal portion of telson and both uropods with moderately large blue-black spots covering dorsal surface, more densely distributed laterally.

Palm and both fingers of cheliped beige, studded with large blue-black spots above that form row between spines of mesial margin of palm; carpus likewise spotted, as also lateral and mesial margins of merus; basis, ischium, and coxa concolorous tan. Remaining pereiopods striped with alternating circular bands of beige-brown and blue-black, latter formed by coalescing dots of pigment; pattern extending from distal coxa to apex of dactyl. Basal podomeres of antennule and antenna beige with irregular blue-black stripe on lateral margins; flagella studded with fine dark spots. No records of ventral coloration available.

Type locality.—Turkey Creek, about 6 mi (9.7 km) northeast of Coffeeville, 0.2 mi (0.3 km) east of State Route 32; T25N, R7E, section 18, Yalobusha County, Mississippi. At this locality, on 23 September 1989, the creek was approximately seven to ten meters wide; generally shallow, ranging from a few centimeters to half a meter in depth; however, in a few places reaching over a meter in depth. The current was slow to moderate and much of the sand bottom was silt-covered. There were numerous snags with varying amounts of detritus caught around their bases. The water was clear upon arrival at the site but soon became turbid from clouds of silt that went into suspension because of collecting activities. The water was 18°C at 1540 hr when the collection was made.

Disposition of types.—The holotype, allotype, and morphotype (USNM 220651, 220652, and 220653, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as is a single paratypic male, Form I. The remaining paratypes (3 ♂I, 4 ♀) are in the Tulane University Museum of Natural History (TU).

Range and specimens examined.—The species is known from only five localities, all in the Yazoo River basin in Mississippi: Calhoun County: (1) Cowpen Creek at St. Rte. 9, 8.6 mi (13.8 km) NNE of Bruce, T11S, R1W, sec. 29, 1 ♂I, 1 ♀, coll. 26 Aug 1989, R.D.S. (TU 6431); Carroll County: (2) Abiaca Creek at St. Rte 17, 0.3 mi (0.5 km) S of Black Hawk (St. Rte. 430), T17N, R3E, sec. 20, 1 ♂I, coll. 27 Sep 1987, R.D.S. (TU 6433); Panola County: (3) Oil Creek, 1.5 mi (2.4 km) E of U.S. Hwy. I-55 on St. Rte 315, T7S, R6W, sec. 30, 1 ♂I, coll. 10 Aug 1967, J. F. Payne, W. G. Anding (USNM 220654); Tallahatchie County: (4) Bellamy Creek, 1.3 mi (2.1 km) S of St. Rte. 32 in Charleston, T25N, R2E, sec. 26, 1 ♀, coll. 27 Oct 1989, R.D.S. (TU 6432); Yalobusha County: (5) type locality, 1 ♂I (holotype), 1 ♂II, (morphotype), 1 ♀ (allotype); 1 ♂I, 2 ♀ (TU 6438), coll. 23 Sep 1989, R.D.S.

Variations.—With so small a type series, observed variation is slight; most is encompassed within the limits expressed in the descriptions of the types, above. The specimens from the type locality seem small by comparison with the other available samples. The carapace lengths of the types are 23.7, 28.1 and 18.5 mm (Table 1), and of the topotypic male, Form I, 21.5 mm, those of the females, 22.2 and 19.5 mm. The carapace length of the Panola County male, Form I is 33.2 mm; while those of the Calhoun County specimens are: male, Form I, 35.8; female, 32.8 mm. The greatest variation noted is in the spinose ornamentation of the cheliped. As noted in the diagnosis, the number of spiniform tubercles along the mesial margin of the palm varies from three to seven; in the morphotype, possibly a juvenile, they are reduced to small rounded tubercles. Although the pattern of distribution of the tubercular ornamentation of the lower mesial margin of the merus varies slightly, the number is consistently three (except the Panola Co. specimen has what appears to be only the broken stump of a proximal third spine on the right side); in contrast, the proximal row of tubercles of the lower lateral margin varies from four to eight. In one male, Form I, and the smallest female from the type locality the cephalic lobe of the epistome is nearly planar and lacks the median ridge; the epistome of the female from Cowpen Creek is similarly developed, but the fovea in the main body is deep, similar to that of the holotype. Also the smallest topotypic female has a bifid spike-like tubercle near midlength of the carpus, and the distal one is acutely spiniform.

Table 1.—Measurements (mm) of *Orconectes* (*Hespericambarus*) *hartfieldi*, new species.

	Holotype	Allotype	Morphotype
Carapace			
Entire length	23.7	28.1	18.5
Postorbital length	17.2	20.6	13.3
Width	11.2	13.0	8.8
Height	10.5	12.7	7.4
Areola			
Length	7.9	9.2	6.1
Rostrum			
Length	7.9	11.0	8.1
Width	4.8	5.5	4.1
Antennal scale			
Length	6.5	7.1	5.6
Width	3.4	3.8	2.8
Right chela			
Length, lateral margin	18.1	18.0	10.1
Length, palm mesial margin	6.4	5.6	4.6
Palm width	8.5	7.5	4.4
Dactyl length	11.2	12.1	6.9
Abdomen			
Length	22.8	31.0	18.0
Width	10.1	12.8	7.5

Environmental notes.—Detailed environmental data are available also for Cowpen Creek (site 1, above) and they differ from those at the type locality. It seems worthwhile to note this range of tolerance for this species.

Cowpen Creek at St. Rte. 9 courses through a narrow, deep, precipitous ravine, and on 26 August 1989, was in low water stage. The stream bed was estimated to be 12.1–15.3 m wide with a channel of water varying from 2.4 to 9.2 m in width. The entire stream bed was compacted clay as was the lower third of the stream bank. There were two ledges in the bed of the stream downstream of the bridge with a 0.6 m drop into a plunge pool. The ledges were undercut in a few places and there were some broken-off pieces in the plunge pool; some crawfish were collected from beneath these ledges and in the pool. The flow was moderate but almost no motion was evident in the pools. There were "cow cakes" in the stream. At 1720 hrs the temperature of the water was 28°C.

Associates.—Crawfishes collected with *Orconectes* (*Hespericambarus*) *hartfieldi* at one or more sites were *Procambarus* (*Pennides*) *ouachitae* Penn, 1956, *Cambarus* (*Lacunicambarus*) sp. ref. *ludovicianus*, and an undescribed member of the genus *Or-*

conectes assignable to the subgenus *Gremicambarus.*

Relationships.—The closest relatives of *Orconectes* (*Hespericambarus*) *hartfieldi* are *O.* (*H.*) *hathawayi* Penn, 1952 and *O.* (*H.*) *perfectus* Walls, 1972. First form males of *O.* (*H.*) *hartfieldi* are easily separated by the presence of a subapical notch or shallow depression on the caudodistal margin of the central projection; the notch is suggested on the male, Form II, but it is not so clearly defined. The annulus ventralis of the female is the most sculptured of the subgenus, and the deep sulcus and long sinus differentiate it from its close relatives. Geographically, the position of *O.* (*H.*) *hartfieldi* in the Yazoo system is between the range of *O.* (*H.*) *perfectus* (Tombigbee system) and *O.* (*H.*) *hathawayi* (southcentral Louisiana).

Etymology.—We take pleasure in naming this crawfish in honor of Paul D. Hartfield, formerly Curator of Invertebrates at the Mississippi Museum of Natural Science, in recognition of his vigorous efforts to collect crawfishes from his state and thus contribute to our knowledge.

Acknowledgments

We express our thanks to the collectors indicated in the "range" comments above for their efforts in securing specimens. Especially we note the constructive criticism of the manuscript by H. H. Hobbs, Jr.

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CHACEUS CESARENSIS, A NEW SPECIES OF FRESH-WATER CRAB (CRUSTACEA: DECAPODA: PSEUDOTHELPHUSIDAE) FROM COLOMBIA WITH A KEY TO THE GENUS

Gilberto Rodriguez and Angel L. Viloria

Abstract.—*Chaceus cesarensis,* new species, adds a sixth species to a genus of pseudothelphusid crabs restricted to high mountains in the Sierra Nevada de Santa Marta, in Colombia, and the Sierra de Perijá, between this country and Venezuela. The distribution of the genus is reviewed and a key is given to separate the known species.

The species of fresh-water crabs composing the genus *Chaceus* Pretzmann, 1965, notwithstanding their phylogenetic interest (Rodriguez & Campos 1989), are poorly known. *Chaceus pearsei* (Rathbun, 1915) was the only species known, until Rodriguez (1980) described a new species, *Chaceus motiloni* (=*Pseudothelphusa* sp. Rodriguez, 1980). In the last ten years knowledge about the genus has been accumulating rapidly and five species are now known (Rodriguez 1980, Campos & Rodriguez 1984, Rodriguez & Bosque 1990), despite the difficulties of collecting in the inaccessible regions of the Sierras of Santa Marta and Perijá inhabited by these crabs. Recently, the junior author had an opportunity to explore the Colombian watershed of the Sierra de Perijá, up to now rarely visited by zoologists. The present paper deals with a new species of the genus found in this area.

Tribe Strengerianini Rodriguez, 1982
Genus *Chaceus* Pretzmann, 1965
Chaceus cesarensis, new species
Fig. 1

Material.—Colombia, Cañón del Rio Manaure, 1 km from Finca El Suspiro, Serranía de Valledupar, Perijá, Departmento del Cesar, 2150 m; 22 Mar 1989; Angel L. Viloria; 1 male holotype, carapace length 11.8 mm, carapace breadth 19.2 mm, fronto-orbital width 12.2 mm, deposited at the Reference Collection, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.

Description.—The carapace is moderately wide (carapace breadth/carapace length = 1.63) relative to other congeners. The cervical groove is straight, thin and shallow distally, wide and deep proximally; it does not reach the margin of the carapace. The antero-lateral border has a slight depression behind the orbit, covered by six low papillae, followed by approximately 15 ill-defined teeth or papillae. The postfrontal lobes are obsolescent, their positions marked only by two slight elevations of the carapace surface; the median groove is represented by a wide, shallow depression. The carapace between the postfrontal lobes and the front is inclined forward, slightly concave in frontal view. The upper margin of the front is slightly convex in dorsal view, not clearly defined except by a slight erosion in this area; the lower margin is almost straight. The front is low, higher toward the sides, advanced.

The larger cheliped has the palm moderately swollen; the fingers do not gape when closed. The exognath of the third maxilliped is 0.75 times the length of the ischium.

The first male gonopod is stocky, its distal

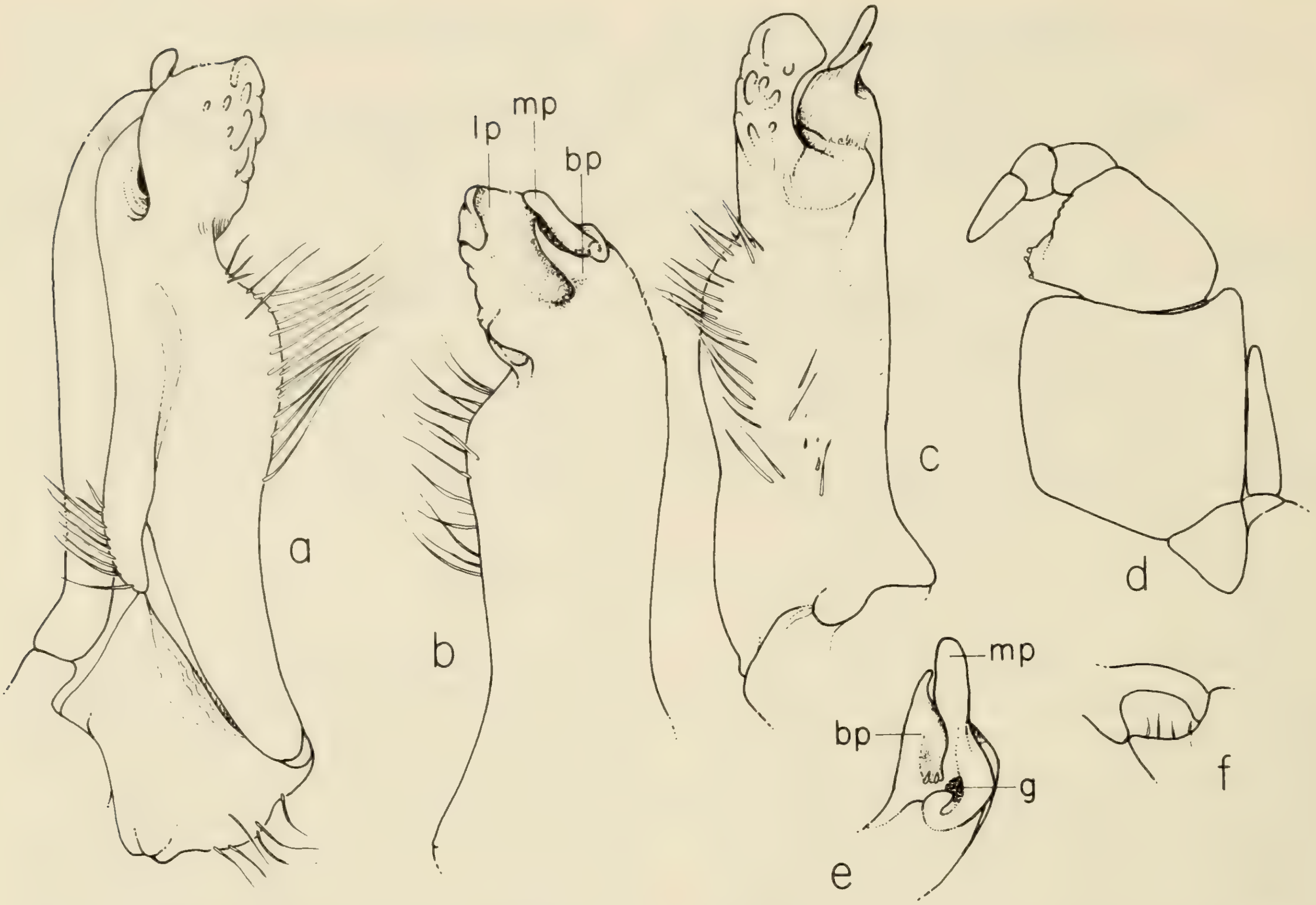

Fig. 1. *Chaceus cesarensis,* new species, holotype: a, Left gonopod, caudal view; b, Same mesial view; c, Same cephalic view; d, Third maxilliped, left; e, Detail of left gonopod gonopore area; f, Aperture of efferent channel; bp, marginal process; g, gonopore; lp, lateral process; mp, mesial process.

end is curved and directed mesially and, consequently, its terminal orifice opens in a plane perpendicular to the main axis of the appendage. The lateral process is well developed, bent over the marginal and mesial processes, with conspicuous and irregular ridges; it reaches the apex of the gonopod. The apical portion consists of a finger-like mesial process and a long, triangular, marginal process. The terminal orifice of the gonopod is surrounded by a few minute spines. There is a row of long plumose setae over the lateral expanded side of the gonopod and shorter setae on the caudal basal surface.

Etymology.—The specific name refers to the type locality in the Departamento del Cesar, Colombia.

Remarks.—*Chaceus cesarensis* resembles both *C. davidi* Campos & Rodriguez, 1984, and *C. pearsei* Rathbun, 1915, in the lateral process of the gonopod which is well developed in relation to marginal and mesial processes. It resembles furthermore *C. pearsei* in the shape and development of the marginal and mesial process. However the present new species differs from all other species of *Chaceus* in the morphology of the lateral process, which is hood-like, and covered with conspicuous irregular ridges on its external surface.

The male holotype, although small, is fully mature, indicating that the present species is of small size as others in the genus.

As several species have been described since the last revision of the genus (Rodriguez 1982), a revised key to the species is presented below. The nomenclature of the processes on the gonopod's apex is shown in Fig. 1.

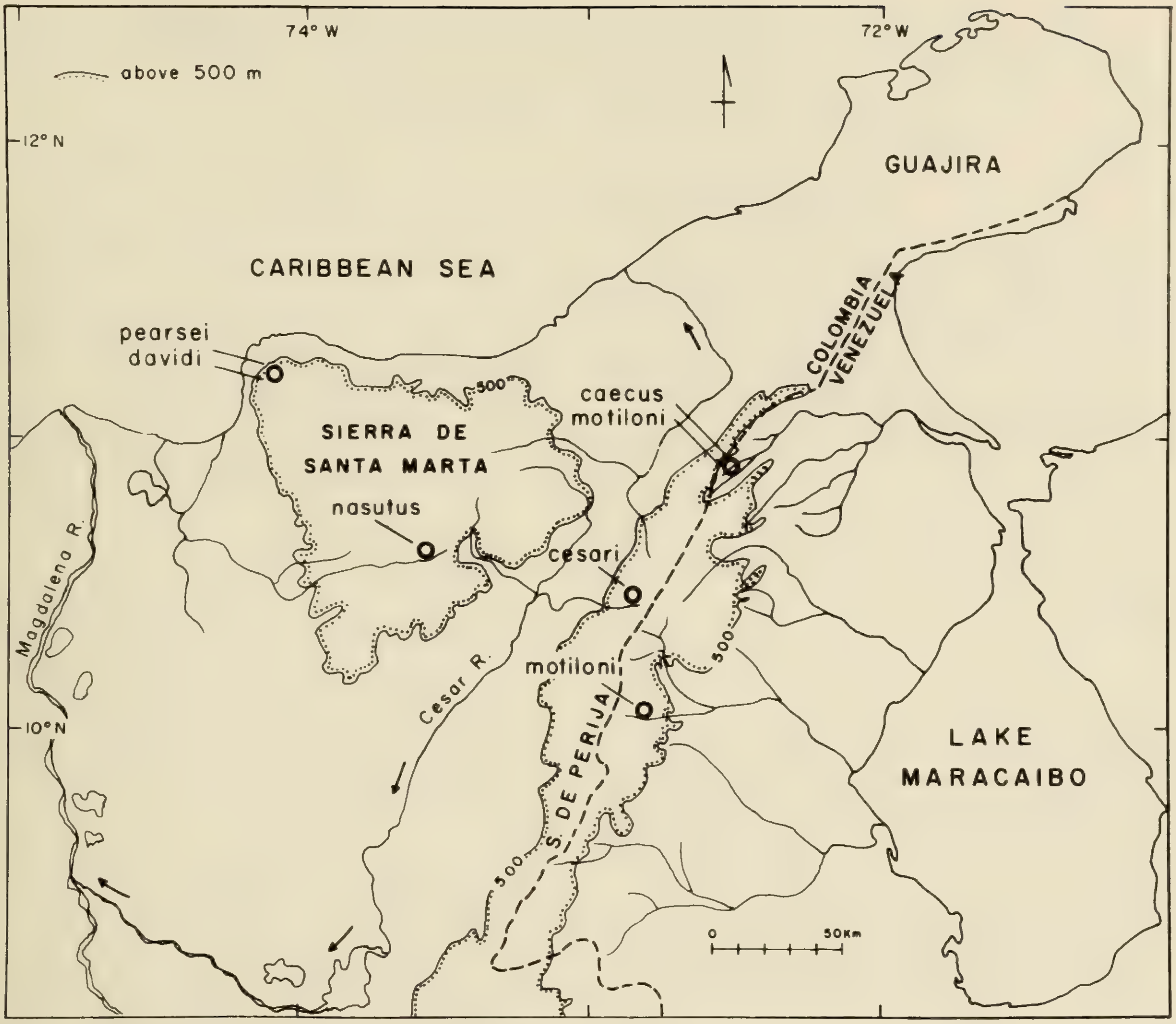

Fig. 2. Geographical ranges of the species of *Chaceus* in Colombia and Venezuela. Only the hydrology relevant to the distribution of the species is shown.

Key to the Species of the Genus *Chaceus*

1. Mesial and marginal processes of first gonopod forming two very elongated projections and directed horizontally .... *C. nasutus*

– Mesial and marginal processes forming a finger-like projection and a basal elongated spine directed mesodistally 2

2. Mesial and marginal processes equally or less developed than lateral processes 3

– Mesial and marginal processes conspicuously more developed than lateral processes 5

3. Mesial and marginal processes very reduced relative to lateral processes .... *C. davidi*

– Mesial, marginal and lateral processes equally developed 4

4. Lateral process subtriangular, with outer surface smooth .... *C. pearsei*

– Lateral process hood-like, with outer surface conspicuously wrinkled *C. cesarensis*

5. Lateral process developed, oval; epigeous species .... *C. motiloni*

– Lateral process rudimentary, foliose; cavernicolous species .. *C. caecus*

The species of *Chaceus* occupy scattered areas in the Sierra Nevada de Santa Marta, Colombia, and the Sierra de Perijá, in the border between Colombia and Venezuela

(Fig. 2), from 590 to 3000 m *Chaceus davidi* Campos & Rodriguez, 1984, and *C. pearsei* (Rathbun, 1915), have overlapping ranges in the northeastern slopes of the Sierra de Santa Marta. *Chaceus nasutus* Rodriguez, 1980, occurs on the southeastern slopes of the same Sierra. The range of *C. motiloni* Rodriguez, 1980, covers the Venezuelan slopes of the Sierra de Perijá, from the headwaters of the Rio Negro to the upper Rio Guasare. *Chaceus caecus* Rodriguez & Bosque, 1990, is known only from a cave located within the range of *C. motiloni. Chaceus cesarensis* is the only species known so far from the Colombian slopes of the Sierra de Perijá.

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REDESCRIPTION OF *CALOCARIDES SOYOI* (YOKOYA, 1933) FROM JAPAN (CRUSTACEA: DECAPODA: AXIIDAE)

Brian Kensley and Tomoyuki Komai

Abstract.—*Calocarides soyoi* is characterized by a carapace with 3–6 lateral rostral spines, (0) 1–4 spines on the median carina, 4–7 spines on the submedian carina, and 6–10 spines on the lateral carina, and by the chelipeds of the first pereopods being strongly tuberculate and having numerous spines on the anterior and posterior margins of the meri. The species has been taken in a depth range of 138 to 270 m off northern Japan.

In 1989–1990 a biological survey of the bottom fishes of the Pacific coast of northern Japan was conducted from the T/V *Tanshu-Maru,* under the auspices of the Japanese Fisheries Agency. A collection of decapod crustaceans captured with a small beam trawl off northeastern Honshu was sent to the second author for identification. Amongst this material were 13 specimens of a fairly large axiid shrimp (total length about 55 mm), which in turn were submitted for identification to the Smithsonian Institution's National Museum of Natural History. The material proved to be a species of *Calocarides,* most likely *C. soyoi* (Yokoya, 1933). Given the abbreviated original description and inadequate figures, it was decided to redescribe the species.

Material has been deposited in the Faculty of Fisheries, Hokkaido University (HUMZ), and in the National Museum of Natural History, Smithsonian Institution (USNM).

Family Axiidae
Calocarides soyoi (Yokoya, 1933)
Fig. 1; Tables 1, 2

Axius soyoi Yokoya, 1933:49, fig. 25.—Horikoshi et al., 1982:30, 33, 38, 39, 120, 145, 168.

Axiopsis (*Axiopsis*) *soyoi:* Sakai, 1987:303.

Calocarides soyoi: Sakai & de Saint Laurent, 1989:4, 83, 103.

Material examined.—HUMZ-C990, 3 ♀ cl 11.3 mm, 14.1 mm, 13.0 mm, off Hachinohe, Aomori Prefecture, 42°52.6′N, 145°22.2′E, 152 m.—HUMZ-C994, ♀ cl 16.9 mm, off Fukushima Prefecture, 37°17.3′N, 141°21.4′E, 141 m.—HUMZ-C998, 3 ♂ cl 12.4 mm, 15.0 mm, 15.3 mm, off Fukushima Prefecture, 37°04′N, 141°31.7′E, 270 m.

USNM 243563, 2 ♂ cl 12.0 mm, 15.0 mm, ovig. ♀ cl 17.9 mm, off Fukushima Prefecture, 37°10.68′N, 141°17.86′E, 138 m.—USNM 243564, ovig. ♀ cl 18.8 mm, ♂ cl 14.2 mm, ♀ cl 11.8 mm, off Hachinohe, Aomori Prefecture.

Description.—Carapace with rostrum reaching to level of proximal antennal article 4, with 3–6 lateral spines, margins continuous posteriorly with lateral carinae bearing 6–10 spines; submedian carina bearing 4–7 spines; median carina bearing (0) 1–4 spines anterior of tubercle. Pleuron of abdominal somite 1 narrow, ventrally rounded; pleura of somite 2–5 ventrally broadly rounded. Telson 1.3 times longer than greatest width; lateral margin with 4 or 5 low serrations, posterolateral corner with 3 mobile small spines; posterior margin with small median spine; 2 pairs submedian fixed spines dorsally.

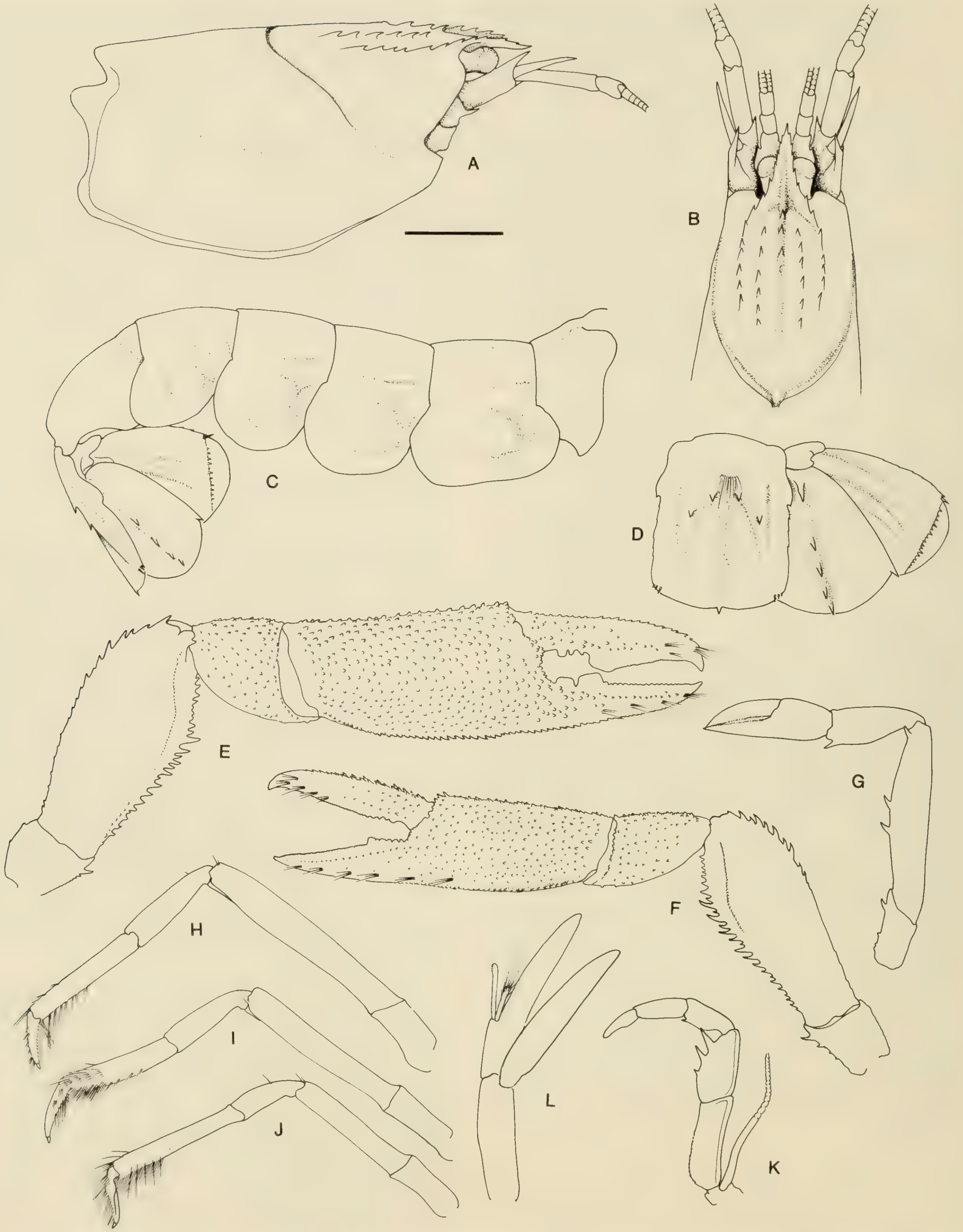

Fig. 1. *Calocarides soyoi:* A, carapace; B, anterior carapace in dorsal view; C, abdomen; D, telson and right uropod; E, pereopod 1, larger cheliped; F, pereopod 1, smaller cheliped; G, pereopod 2; H, pereopod 3; I, pereopod 4; J, pereopod 5; K, maxilliped 3; L, male pleopod 2. Scale for A–K, 5.0 mm, for L, 1.0 mm.

Table 1.—Distribution of exopods, epipods, and gills in *Calocarides soyoi.* r = reduced.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
Setobranch	—	—	1	1	1	1	1	1

Eye reaching to about midlength of rostrum, poorly pigmented. Antennal acicle slender, elongate, falling just short of distal articulation of article 4 of peduncle. Maxilliped 3, ischium with fine serrations along posterior margin; merus with 3 strong spines on posterior margin increasing in length distally; carpus with small posterodistal spine. Pereopod 1, larger cheliped with ischium having single distal spine and several serrations on posterior margin; merus with proximal part of anterior margin bearing low serrations, distal part bearing 8–10 spines, posterior margin spinose for whole length, spines longest in midlength region; carpus with lateral, anterior, and most of mesial surfaces bearing small subacute tubercles; propodal palm about 1.5 times length of fingers, entire surface fairly densely covered with small acute and subacute tubercles, cutting edge of fixed finger with 2 strong square tubercles proximally, followed by regular row of tiny crenulations; dactylus with anterior margin serrate, lateral surface granulate, cutting edge proximally concave, with 3 small and one broad tubercles followed by regular row of tiny crenulations. Smaller cheliped with ischium, merus, and carpus less robust than, but similar to, those of larger cheliped; propodal palm about 1.3 times length of fingers, cutting edge of fixed finger with about 6 small tubercles proximally followed by regular row of tiny crenulations; dactylus with few low tubercles proximally on cutting edge followed by regular row of tiny crenulations. Pereopod 2, ischium with 2 low proximal tubercles and stronger distal spine on posterior margin; merus with 2 or 3 strong spines at about midlength and single distal spine on posterior margin; carpus with single posterodistal spine. Pereopods 3–5 lacking ischial and meral spines. Distribution of exopods, epipods, and gills, see Table 1. Pleopod 1 in male absent; uniramous in female. Endopod of pleopods 2–5 bearing appendix interna. Pleopod 2 in male with setose appendix masculina shorter than appendix interna. Lateral ramus of uropod with lateral margin bearing about 5 low distal serrations, mobile spine at articulation of suture, about 16 small spines along suture; mesial ramus with strong laterodistal

Table 2.—Carapace spination in *Calocarides soyoi.*

	Carapace length mm	Median carina spines	L/R submedian carina spines	L/R lateral carina spines	L/R rostral spines
ovig. ♀	18.8	2	6/5	7/7	5/6
ovig. ♀	17.9	3	6/6	8/7	5/4
♀	16.9	2	6/6	8/8	4/4
♀	14.1	4	4/6	6/6	3/5
♀	13.0	4	6/6	6/6	4/4
♀	11.8	4	5/4	8/7	5/4
♀	11.3	2	6/6	7/8	5/6
♂	15.3	2	5/5	8/7	4/5
♂	15.0	4	7/7	7/8	5/5
♂	15.0	3	6/5	10/10	4/4
♂	14.2	2	5/6	6/6	3/4
♂	12.4	2	4/5	—	—
♂	12.0	1	5/6	7/6	5/5

spine, dorsal longitudinal ridge bearing strong proximal spine and 4 spines on distal half.

Egg size: 1.7 × 2.0 mm, slightly ovate.

Color in life: Entire animal orange-brown, with lateral carapace and abdomen somewhat paler. Cornea pale yellow.

Remarks.—Few records of species of *Calocarides* (or of genera confused with *Calocarides*) exist for Japan (see List of Japanese Thalassinidea in Sakai 1987:303).

Kobjakova's record of *Calastacus quinqueseriatus* (1937:142, pl. 2, fig. 8) from the Sea of Japan appears from the figure to be fairly similar to the present species, but does not have spinose margins on the first chelipeds; these latter are also proportionally broader than in true *C. quinqueseriatus* or in the present species.

The present species differs from *C. quinqueseriatus* (Rathbun, 1902) known from Oregon to southern California, in having somewhat less slender first chelipeds, smaller and more numerous spines on the anterior margin of the propodi of the first chelipeds, anterior margins of the dactyli of the first chelipeds spinose for their whole length, rather than having just a few proximal spines, and in being a smaller species (cl ovig. ♀ *C. quinqueseriatus* 15.4–24.0 mm).

Axius habereri Balss, 1913, (see also Balss 1914) reported from Japan and Korea, is probably not a *Calocarides,* given the broad non-tubercular first pereopods and the presence of a post-cervical middorsal carina.

The species recorded by Yokoya (1933) as *Axius soyoi,* from Fukushima (almost exactly the same locality as the present species) appears to be very similar to the present species. The major difference mentioned in the description is that the median carina lacks any spines or tubercles. Yokoya's description and figures are, unfortunately, insufficiently detailed, especially in the nature of the first chelipeds, the uropods and telson. Yokoya's species was based on ten specimens; no holotype was designated. The second author attempted to trace these syntypes, from Tokyo Imperial University through Kyushu University, to Kitakyushu Museum where a single syntype was located. This dried and damaged specimen proved to be something other than a *Calocarides* species, with four distinctive spines on the lateral cervical groove, and four spines on the anterolateral margin of the carapace. Several possibilities now present themselves: Yokoya had more than one species amongst the ten specimens, or, the supposed extant syntype is some other species whose data or labels were misplaced in the several moves of the *Sôyô-Maru* material, or, the true syntypes still exist and may be brought to light.

We have decided to take a conservative position, and refer to the present material as *Calocarides soyoi.* We consider the possibility remote that two different species of *Calocarides* occur in the same depth-range in the same localities off the Fukushima Prefecture. We have not selected a neotype, as there is still a distinct possibility that Yokoya's syntypic material will be found. Amongst the present 13 specimens, there is some variation in the spination of the carapace (see Table 2). The lateral and submedian carinal spine counts agree well with those given by Yokoya. The median carinal spination ranges from one to four spines; given this variation, it seems possible that some specimens may lack spines on this carina entirely, as in Yokoya's material.

Acknowledgments

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A NEW GERYONID CRAB FROM WALTERS SHOALS, SOUTHWESTERN INDIAN OCEAN (CRUSTACEA: DECAPODA: BRACHYURA)

Raymond B. Manning

Abstract.—*Chaceon collettei,* the fifth species of the genus to be recognized from the southwestern Indian Ocean, is described from material collected in 1090–1100 meters at Walters Shoals. It most closely resembles *C. paulensis* (Chun) from Amsterdam and St. Paul islands, central Indian Ocean, and differs from other species reported from the area in having well developed anterolateral spines on the carapace in adults.

Among the specimens collected during Cruise 17 of the Russian vessel *Vityaz* in the southwestern Indian Ocean in 1988 were specimens of a large geryonid crab that resembled *Chaceon paulensis* (Chun, 1903) in having well developed frontal and anterolateral spines on the carapace in adults. Comparison of these specimens with material of *C. paulensis* showed that they were distinct. The material from Walters Shoals is named here.

The holotype and two paratypes have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and a paratype is in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHNP). Abbreviations used below include: cb, carapace width including anterolateral spines; cl, carapace length on midline; leg, collector; m, meters; mm, millimeters; P5, fifth pereopod (fourth walking leg); sta, station.

Chaceon collettei, new species
Figs. 1a–h, 2

Material.—Indian Ocean: Walters Shoals, 33°01.6′–33°04′S, 44°49.2′–44°49.1′E, 1090–1100 m, *Vityaz* Cruise 17, sta 2670, leg B. Collette, 19 m shrimp trawl, 8 Dec 1988: 2 ♂, 2 ♀. Larger ♂, cl 112 mm, cb 143 mm, is holotype (USNM 252412), smaller ♂ and 1 ♀ are paratypes (USNM 252411), 1 ♀ is paratype (MNHNP B.24528).

Diagnosis.—A large *Chaceon,* cl to 112 mm, cb to 143 mm, with 5 sharp anterolateral teeth on the carapace in adults and with laterally compressed dactyli on the walking legs. Carapace 1.3 times broader than long, moderately inflated at protogastric regions, convex from front to back. Frontal teeth sharp and elongate, medians extending further forward than laterals; distance between submedian frontal teeth less than distance from submedian to lateral frontal teeth. Distance from first to second anterolateral teeth less than distance from third to fourth, distance from first to third anterolateral teeth subequal to distance from third to fifth (slightly less to slightly greater). Carapace smooth, with few, shallow scattered pits dorsally, branchial regions slightly more pitted and eroded than remainder of surface, hepatic regions smooth. Orbit shallow, depth half width. Suborbital tooth long and sharp, extending to or beyond apices of outer frontal teeth; suborbital margin smooth. Outer angle of merus of third maxilliped projecting laterally. Cheliped merus with sharp spine subdistally and sharp spine to blunt lobe distally; carpus with spiniform granules dorsally and distal outer spine, anterior margin smooth; propodus with distal spine dorsally, rounded off in large male.

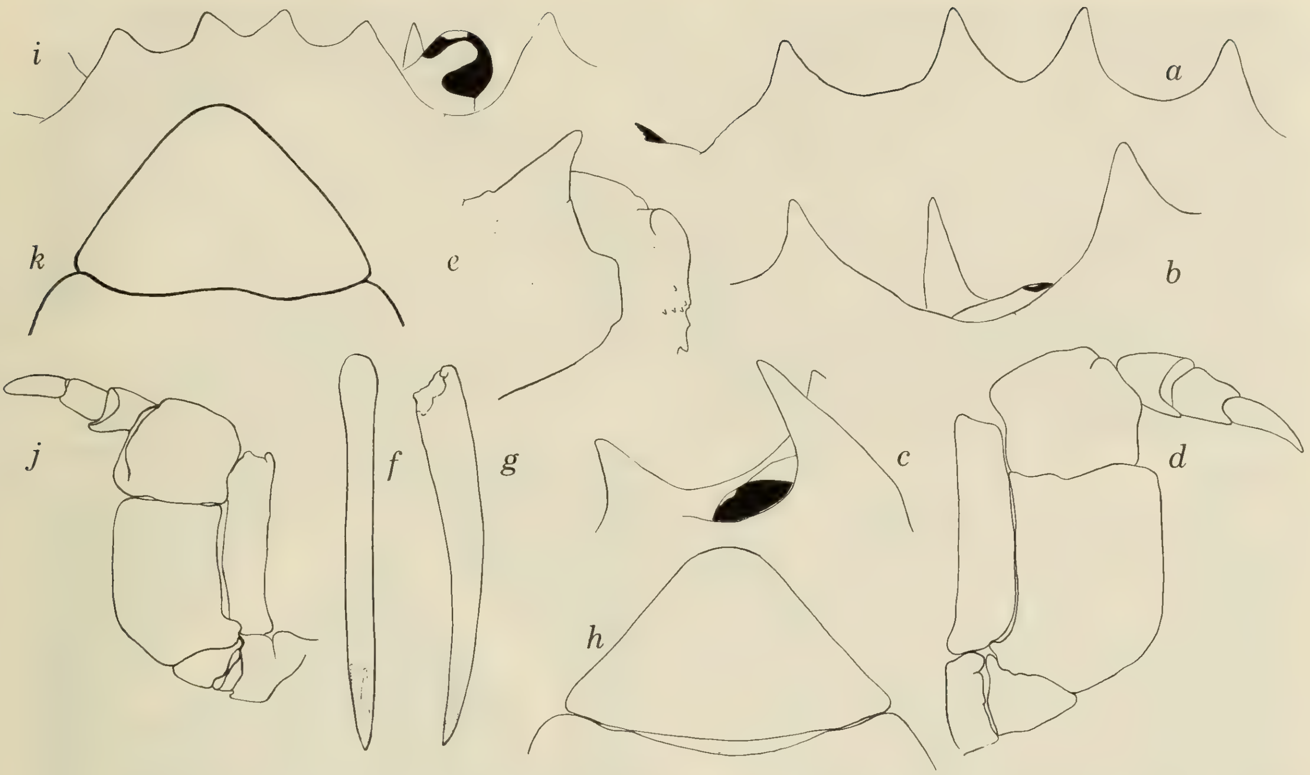

Fig. 1. a–h, *Chaceon collettei,* n. sp., male holotype, cl 112 mm, Walters Shoals. a, Front; b, Orbit; c, Ventral view of orbit; d, Third maxilliped; e, Distal end of merus of fifth pereopod; f, Dactylus of fifth pereopod, dorsal view; g, Dactylus of fifth pereopod, posterior view; h, Telson of male. i–k, *Chaceon paulensis* (Chun), male, cl 82 mm, St. Paul island. i, Frontal region; j, Third maxilliped; k, Telson of male.

Meri of posterior three walking legs each with strong distal spine dorsally. Dactylus of walking legs laterally compressed, height at midlength greater than width, tips of dactyli sharp. P5: merus 3.4 times longer than high in female, 4.9–5.2 times longer than high in males, length 0.6 times cb in both sexes; carpus with line of erect spinules dorsally; propodus 4.4 times longer than high in males (broken in females); dactylus relatively short, 0.83–0.84 times as long as propodus. Telson length 0.6 times width.

Size.—Males, cl 100 and 112 mm, cb 128 and 143 mm; females, cl 87 and 88 mm, cb 113 and 117 mm.

Color.—Color in life was not recorded, but preserved specimens are pink, suggesting that this species, like *C. paulensis,* is red in life.

Remarks.—*Chaceon collettei* is the fifth species of the genus to be recognized from the southwestern Indian Ocean. It resembles *C. paulensis* (Chun, 1903) from Amsterdam and St. Paul's islands and differs from *C. chuni* (Macpherson, 1983) from Namibia and South Africa, *C. crosnieri* Manning & Holthuis, 1989 from Madagascar, and *C. macphersoni* (Manning & Holthuis, 1988) from Madagascar and southwestern Africa in having well developed frontal and anterolateral spines on the carapace in adults and in having a sharp distal spine dorsally on the merus of the walking legs. This new species differs from *C. paulensis* (Fig. 1i–k) in several characters: the frontal teeth are sharper and slenderer, the orbit is shallower, the outer angle of the merus of the third maxilliped projects further laterally, the fourth anterolateral tooth of the carapace is smaller, and the telson of the male is wider.

Although geryonid crabs have relatively restricted ranges (Manning & Holthuis 1989: 74), a comparison of *C. collettei* with species from outside the Indian Ocean is still useful. One other species from the Indo-West Pa-

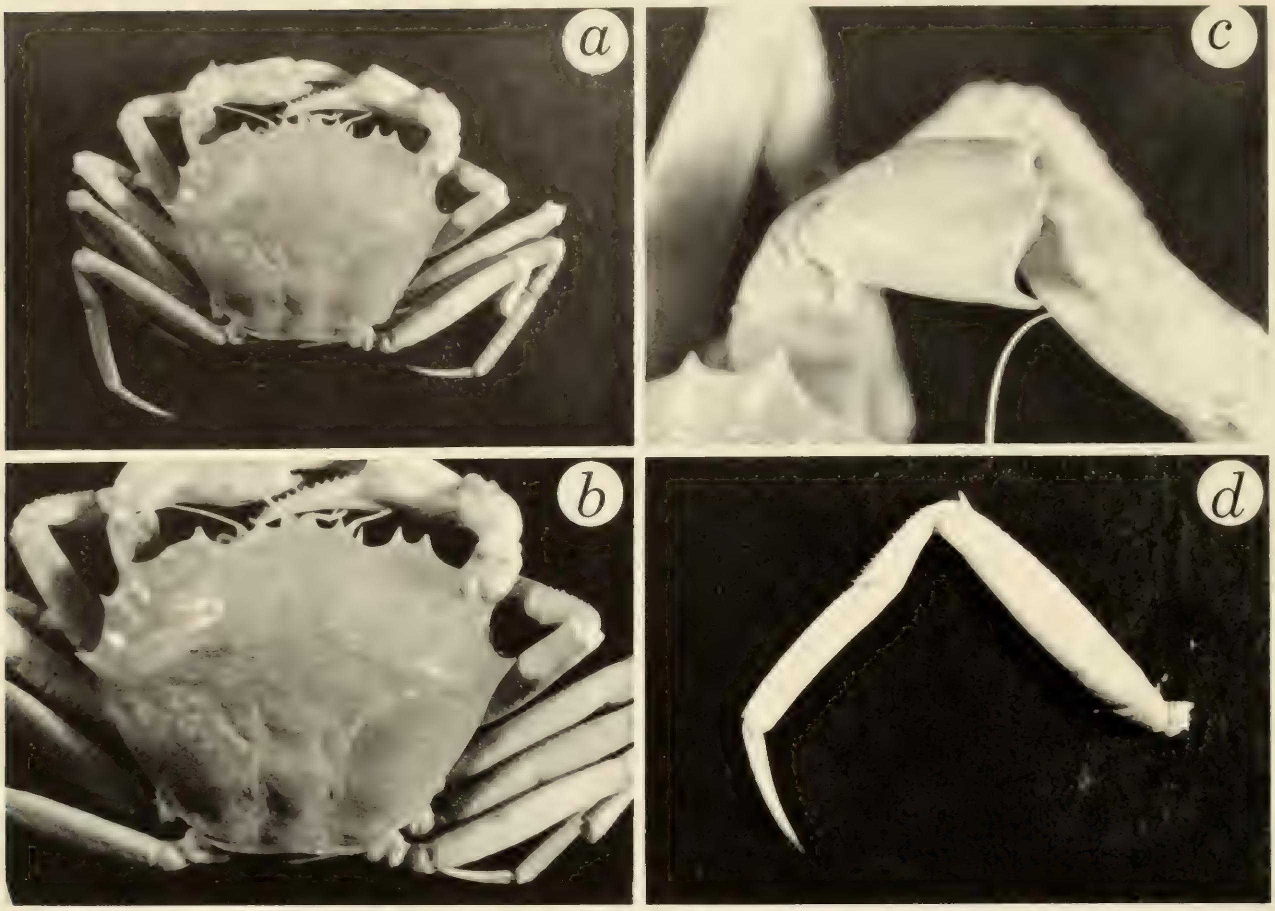

Fig. 2. *Chaceon collettei,* n. sp., male paratype, cl 100 mm. a, Dorsal view; b, Carapace, enlarged; c, Carpus of cheliped; d, Fifth pereopod.

cific, *C. yaldwyni* Manning, Dawson & Webber, 1990 has a distal dorsal spine on the merus of the walking legs; it differs from *C. collettei* in having much smaller and blunter anterolateral teeth on the carapace in adults.

Of the four species from the Atlantic with relatively sharp anterolateral teeth on the carapace and laterally compressed dactyli on the walking legs, three, *C. atopus* Manning & Holthuis, 1989 from St. Helena, *C. inghami* (Manning & Holthuis, 1986) from Bermuda, and *C. inglei* Manning & Holthuis, 1989 from the northeastern Atlantic, differ from *C. collettei* in having much slenderer walking legs, with the merus more than six times longer than high. In the fourth species, *C. gordonae* (Ingle, 1985) from the Cape Verde Islands, the spines of the carapace are much smaller in adults.

Little is known about the decapods of Walters Shoals, an area about 400 miles south of Madagascar and 600 miles from the African coast (Kensley 1969). Kensley (1969, 1981) listed five species of decapods from there, including one endemic species, *Alpheus waltervadi* Kensley, 1969, all from shallow water, in 38–46 meters.

Name.—This species is dedicated to Bruce B. Collette, Systematics Laboratory, National Marine Fisheries Service, who participated in the *Vityaz* cruise during which this species was collected and who enriched the national collections with material from that cruise.

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SEROLIS APHELES, A NEW SPECIES (ISOPODA: SEROLIDAE) FROM THE SOUTHWEST INDIAN OCEAN, AND A RANGE EXTENSION FOR *SEROLIS ANTARCTICA* BEDDARD, 1884

Marilyn Schotte

Abstract.—*Serolis apheles,* a new species of deepwater marine serolid isopod from the Madagascar Plateau, is described. Diagnostic features include absence of eyes, small size relative to that of cogeners, smooth dorsum, and coxal plates on pereonite 6 that extend posteriorly, nearly to the apex of the pleotelson. A new locality record for *Serolis antarctica* Beddard, 1884, extends its range in the Indian Ocean from sub-Antarctic waters off Crozet Island to the Natal Basin off Mozambique. It has not been otherwise recorded since first collected in 1873 during the *Challenger* Expedition.

The family Serolidae contains more than 80 currently known species, 22 of which are found in the Indian Ocean (down to 60 degrees South) from shallow water to abyssal depths. Thirteen of these (in the genera *Serolis* and the closely-related *Serolina*) have been described from coastal areas off south and western Australia (Poore 1987). *Serolis apheles* is the second in the genus to be found in South African waters; *Serolis brinki* Kensley, 1978 was discovered off Natal. The remaining eight Indian Ocean species (*Ceratoserolis trilobitoides* (Eights, 1833); *S. antarctica* Beddard, 1884; *S. aspera* Sheppard, 1933; *S. bromleyana* Suhm, 1876; *S. latifrons* White, 1847; *S. monodi* Cals, 1979; *S. quadricarinata* White, 1847; and *S. septemcarinata* Miers, 1875) have been recorded near the Prince Edward, Crozet, and Kerguelen islands in surrounding deep-water basins. *Serolis cornuta* Studer, 1879 from Crozet and Kerguelen Islands, has been synonymized by Brandt (1988) with *C. trilobitoides.* The material dealt with in this paper was collected during the 1964 cruise of the International Indian Ocean Expedition (IIOE) research vessel *Anton Bruun.* The new species was collected at 950 m on the Madagascar Plateau. Later that year a specimen of *S. antarctica* was collected at 875–890 fathoms (1601–1629 m) off the coast of Mozambique near the Natal Basin.

Both specimens treated herein are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Serolis apheles, new species
Figs. 1A–H, 2A–G, 3A–F

Material examined.—USNM 252414, Holotype male, TL 5.6 mm IIOE R/V *Anton Bruun* cr. 7, sta 380-C, Menzies trawl, 32°58′S, 43°41′E, 950 m, 30 Aug 1964.

Diagnosis.—Body slightly longer than wide, nearly circular in outline, lacking dorsal tubercles and spines. Head with anterolateral angles acute, slightly produced, anterior margin emarginate with small medial projection and tiny projection to each side. Eyes absent.

Coxal plates demarked by sutures on pereonites 2 to 4. Coxal plate 5 extending slightly beyond third pleonite; that of pereonite 6 extending almost to apex of pleotelson. Pleotelson as long as broad, without ornamentation, slightly vaulted and broadly rounded, with obtuse angle apically.

Antennular flagellum of 29–30 articles. Antennal peduncle nearly reaching poste-

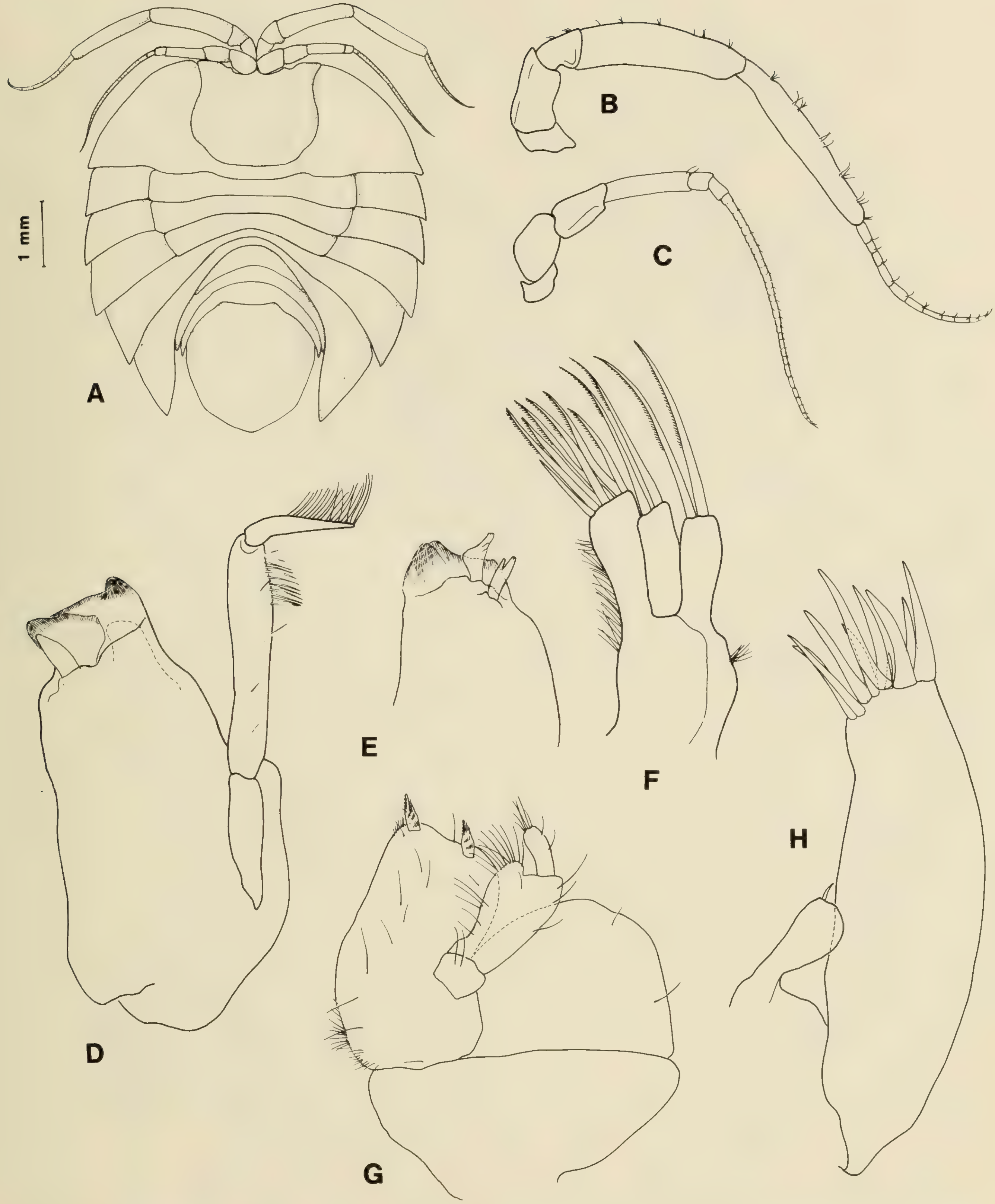

Fig. 1. *Serolis apheles* male. A, dorsal habitus. B, antenna. C, antennule. D, left mandible. E, cutting edge of right mandible. F, second maxilla. G, maxilliped. H, first maxilla.

rior margin of pereonite 1, flagellum of 14 articles. Mandibles, maxillae and maxilliped as figured, typical of genus.

Propodus of pereopod 1 having alternating slender bifid setae and broad setulose setae; carpus with 2 stout, bristly, hooked setae on distal margin. Propodus of male pereopod 2 with 5 stubby setae proximally

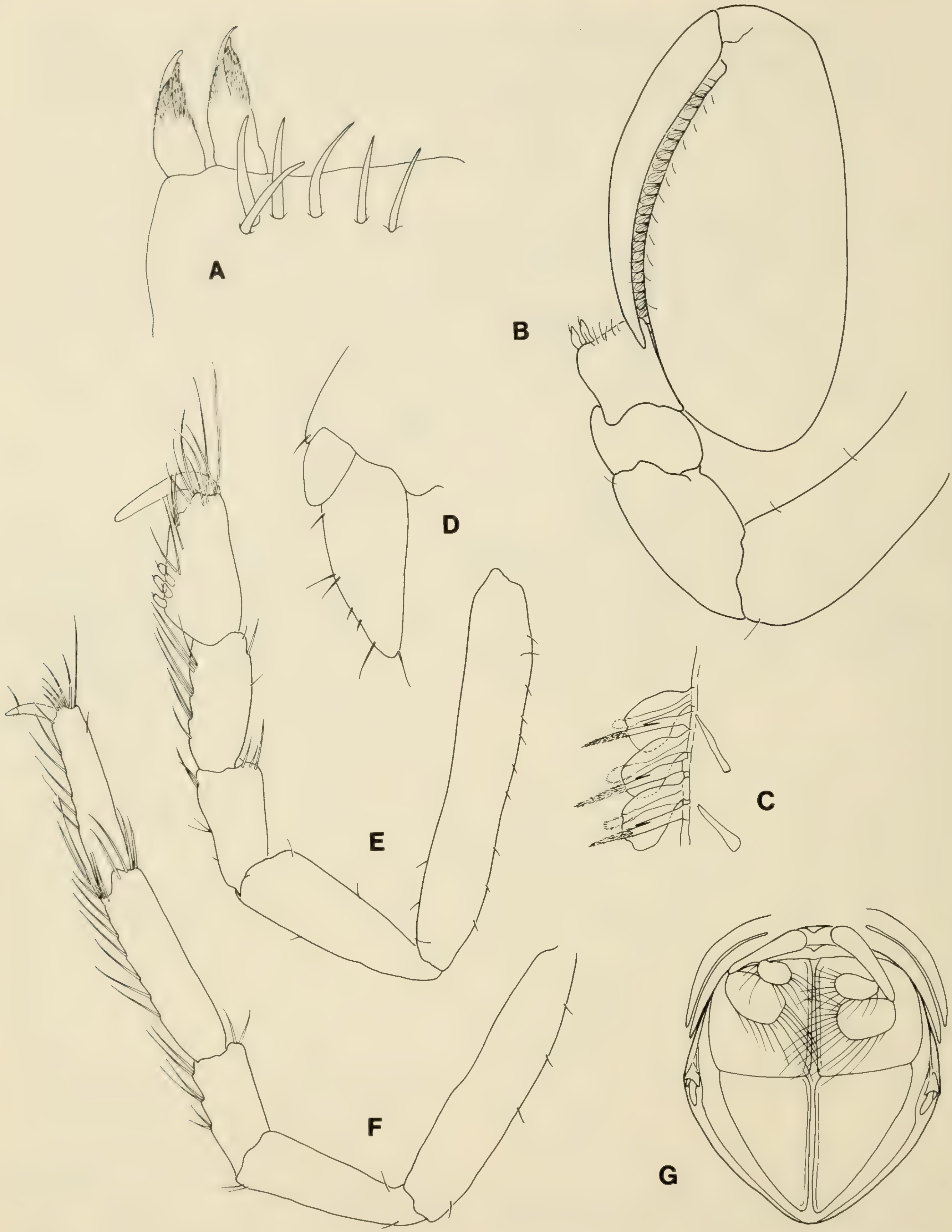

Fig. 2. *Serolis apheles* male. A, detail of distal edge of carpus, pereopod 1. B, pereopod 1. C, detail of armature on propodus of pereopod 1. D, uropod. E, pereopod 2. F, pereopod 7. G, ventral pleotelson.

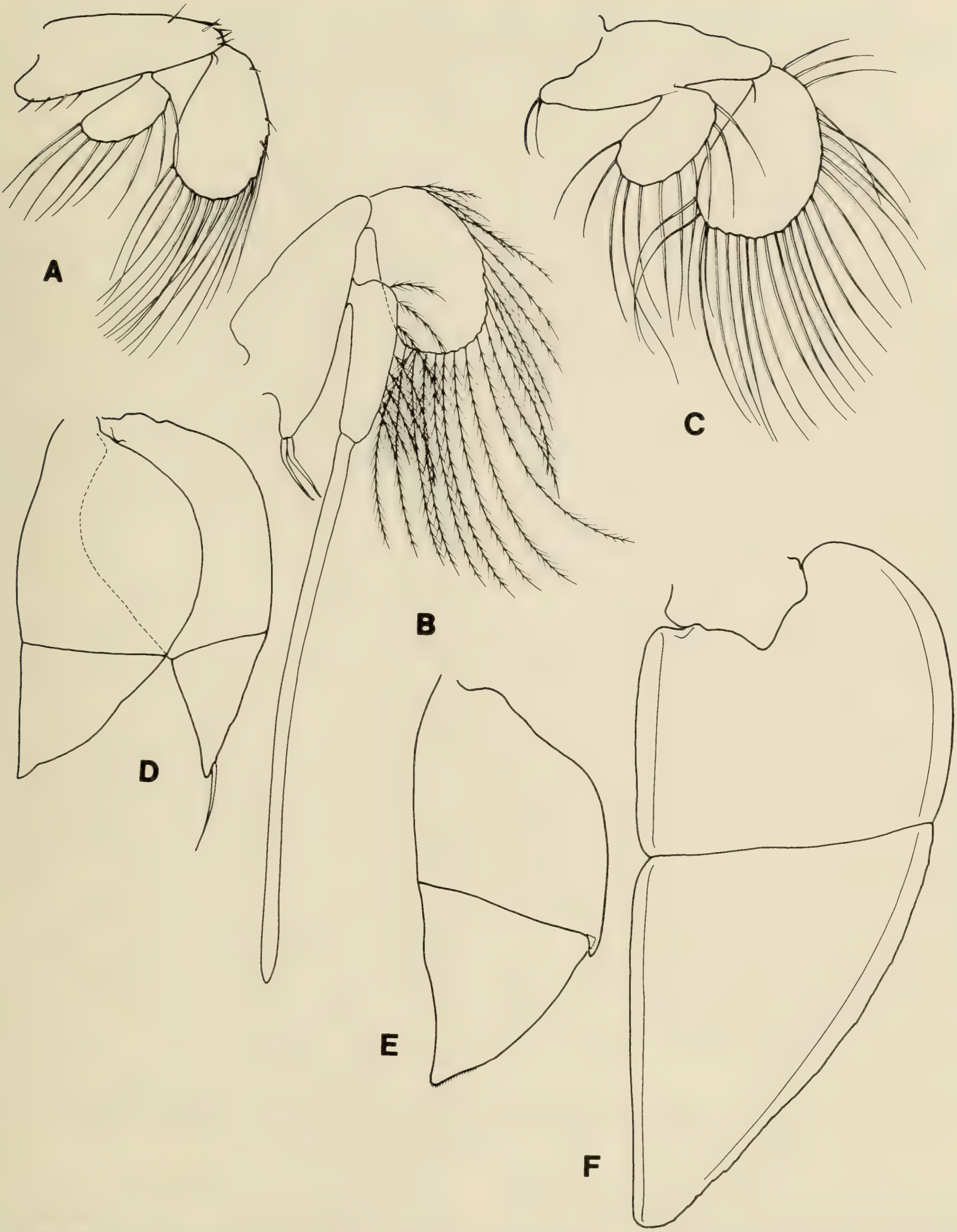

Fig. 3. *Serolis apheles* male. A, pleopod 1. B, pleopod 2. C, pleopod 3. D, pleopod 5. E, F, endopod and exopod of pleopod 4.

on inner margin; propodus and carpus with many long setae, sometimes paired. Pereopod 7 having many long setae on distal margin of propodus and on inner margin of propodus and merus.

Pleopods 1 and 3 with subelliptical rami, exopods nearly twice as long as endopods. Appendix masculina of second male pleopod 3.4 times length of endopod. Both rami of pleopod 4 with tranverse sutures near midpoint; both rami of pleopod 5 with sutures at distal two-thirds of lengths. Uropods small and ventral, not visible dorsally; exopod about one-third length of endopod.

Remarks.—The new species can be distinguished from all its cogeners by the combination of small size at maturity, the lack of any sculpture on the dorsum, absence of eyes, and the length of the coxal plates on pereonites 5 and 6 relative to the pleotelson. It is similar in shape to *S. margaretae* Menzies, 1962, collected off Tierra del Fuego, but lacks the eyes and pleotelsonic middorsal carina found in the latter. *S. brinki* also recorded off southeastern Africa, is also blind but does not possess the extended coxal plates found in the new species. *S. monodi* Cals, 1979, lack eyes and has reduced uropods like *S. apheles;* likewise, it has little dorsal ornamentation except on the pleotelson, whose sculpturing separates it readily from the new species.

Etymology.—The specific name is derived from the Greek "apheles" meaning "smooth, simple," characterizing the unadorned integument.

Serolis antarctica Beddard, 1884
Fig. 4A–C

Serolis antarctica Beddard, 1884a:333–334; 1884b:plate III, figs. 1–6.

Material.—USNM 252417, 1 female, TL 31.5 mm, IIOE R/V *Anton Bruun* cr. 7, sta 369 F, Agassiz trawl, 24°04′S–24°07′S, 36°15′E–36°11′E, 1611–1629 m, 17 Aug 1964.

Previous records.—Southern Indian Ocean, between Prince Edward Island and Crozet Islands: 46°46′S, 45°31′E to 46°16′S, 48°27′E, 2516–2928 m; off Pernambuco, Brazil: 9°10′S–34°49′W, 732 m (Beddard 1884b).

Remarks.—The three syntypes of *S. antarctica* (one male, two females) from BMNH were examined and compared with the present specimen; obvious variations can be seen as well as identical features (see Fig. 4A–C). The mouthparts, antennal bases, keeled sternites, pleopods (female), and uropods seem to be identical. Antennal flagellae could not be counted since in the types there are no such whole appendages. In the Natal Basin specimen, a female, the second and third pleonites extend beyond the midpoint of the telson; the sixth coxal plates extend beyond its apex by a quarter of its length. Small, densely opaque areas, perhaps retaining vestiges of facets, appear where the eyes should be but are probably non-functional. The dorsum has no middorsal tubercles on the somites as seen in Beddard's types and the degree of dorsal reticulation in general is much less although still evident. In the type specimens there are no vestigal eyes but raised areas exist in that position. The pleonites do not extend beyond the midpoint of the telson and the sixth coxal plates do not extend beyond its apex although they appear somewhat longer in the male. The types have keels along the outer edge of the first coxal plates and are absent in the present specimen, which is also considerably broader than the female types. Sculpturing and ornamentation of the telson, key features in separating serolids, seem to be identical in both variants.

Sexual dimorphism and variation in coxal plate extension have been illustrated in other serolids, e.g., *S. gracilis* Beddard, 1884b and *S. bromleyana* Suhm, 1876. Dorsal tuberculation has been shown to vary among conspecifics of the *S. minuta* group (Holdich & Harrison 1980). The present specimen is assigned for now to the species *S. antarctica* in light of evidence that se-

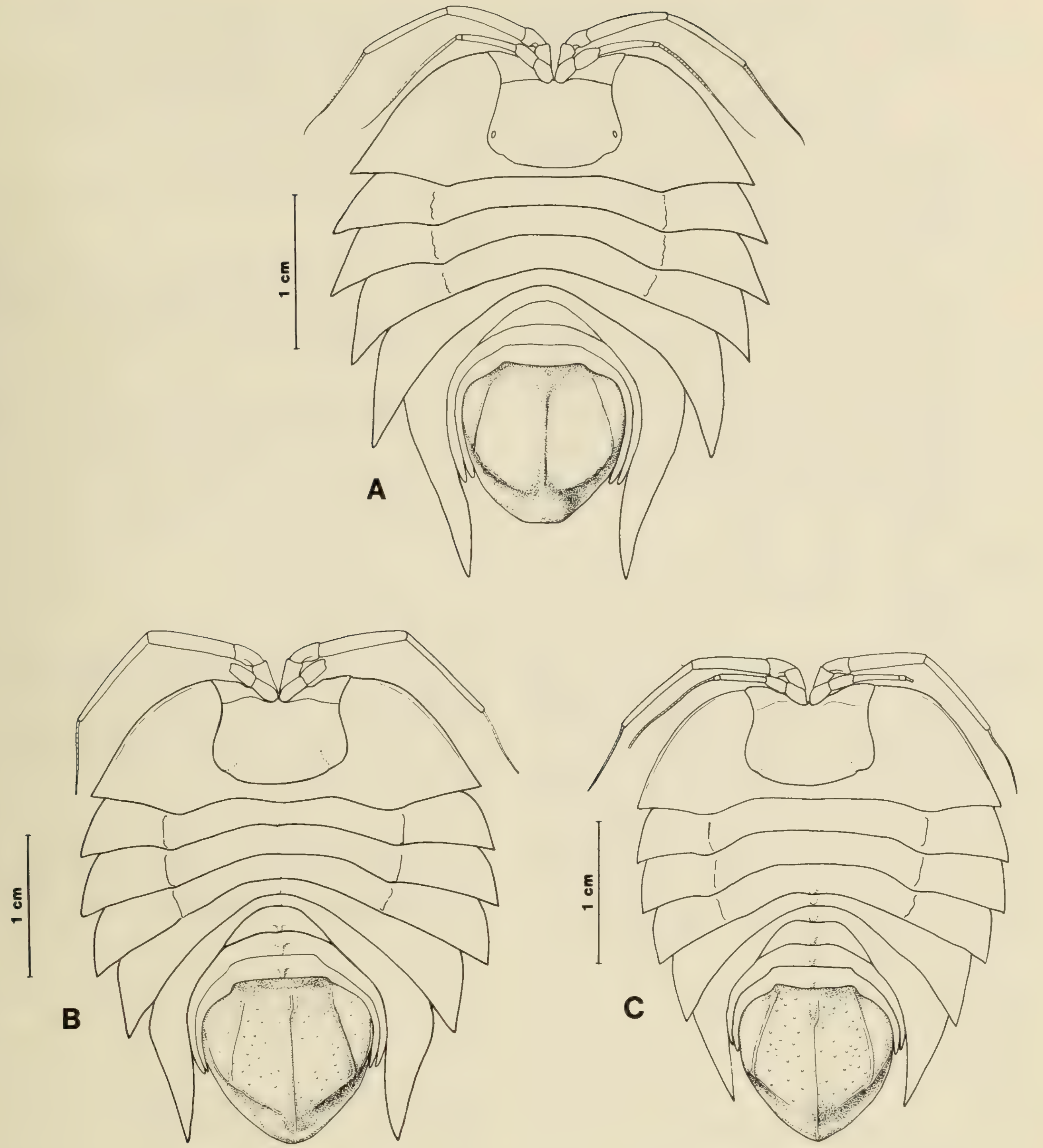

Fig. 4. *Serolis antarctica.* A, female, from Natal Basin, off Mozambique, habitus. B, male syntype, from off Kerguelen Island, habitus. C, female syntype, same locality, habitus.

rolids have a known potential for intraspecific morphological variation, especially when different lots may represent extremes of the geographical range. The current record represents a considerable northerly extension of the species' range in the Indian Ocean and suggests that the Natal Basin is connected to sub-Antarctic waters at abyssal depths. The original description of *S. antarctica* is based on material collected during the *Challenger* Expedition (1873) from stations near the Crozet Islands at 2516–2928 m (the syntypes) and from off Pernambuco, Brazil at 732 m (Beddard 1884b). The latter specimen was not examined. Hitherto there have been no records of *S. antarctica* since Beddard's original report.

Acknowledgments

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DESCRIPTION OF THE PELAGIC COPEPOD, *CTENOCALANUS HERONAE* VEGA-PÉREZ AND BOWMAN, FROM OFF SÃO PAULO, BRAZIL (CALANOIDA: CLAUSOCALANIDAE)

L. Amelia Vega-Pérez and Thomas E. Bowman

Abstract.—*Ctenocalanus heronae* is described from Atlantic waters of the Ubatuba region, São Paulo state, Brazil. It is distinguished by its short antennae 1, the form of the genital segment, and the number and form of the ctenospines on leg 4.

Resumen.—Una nueva especie, *Ctenocalanus heronae,* es registrada para las aguas de la región de Ubatuba, Estado de São Paulo, Brasil. Esta espécie puede ser reconocida por la antena 1 corta, el segmento genital y el número y forma de las ctenoespinas de la pata 4.

The genus *Ctenocalanus* was established by Giesbrecht (1888) for a small calanoid collected in the eastern tropical Pacific (14°N, 132°W), *Ctenocalanus vanus.* Giesbrecht's species was reported subsequently from numerous localities in warm waters of the Atlantic, Pacific, and Indian Oceans. It has also been reported from cold waters (e.g., Farran 1929, Vervoort 1951, Tanaka 1960, 1964, Senô et al. 1963) but these reports are not supported by descriptions or illustrations and cannot be accepted without confirmation. We believe it likely that these authors had *C. citer* rather than *C. vanus.* Until recently all published records of *Ctenocalanus* were attributed to *C. vanus* except four reports (Mori 1937, Honjo et al. 1957, Andronov & Maigret 1980, Alvariño 1989) that recorded *C. longicornis* Mori, 1937. Alvariño's specimens were from off southern California; those of Andronov & Maigret were from northern Mauritania; those of the other three authors were from off Japan. According to Mori (1937) *C. longicornis* differs from *C. vanus* in lacking leg 5 in the female (the male was not found) and in its longer antenna 1. However, the ratio antenna 1 length : body length shown by Mori (1937:pl. 15, fig. 16) is very close to that shown by Giesbrecht (1892:pl. 36, fig. 28). Tanaka (1956), without any discussion, placed *C. longicornis* in synonymy with *C. vanus,* but we believe the validity of his action requires further study. We consider the present status of *C. longicornis* to be uncertain.

More recently three additional species of *Ctenocalanus* have been reported: *C. citer* Heron & Bowman (1971) from the Pacific sector of the Antarctic, and two species from the Gulf of Elat (Aqaba) described by Almeida Prado-Por (1984), *C. campaneri* and *C. tageae.*

Björnberg (1963) reported but did not name two forms of *C. vanus* from Brazilian waters, a larger form (1.35 mm) with shorter first antennae from colder waters, and a smaller form (1.16–1.26 mm) with longer first antennae. No illustrations were provided, but in 1982 Björnberg again reported these two forms from Brazil and gave illustrations of the female genital segment of both forms and of leg 5 in lateral view of the larger form.

Specimens of a *Ctenocalanus* from waters of the Ubatuba region, off São Paulo state, Brazil, differ from previously described species of *Ctenocalanus* and were briefly diagnosed as *C. heronae*, new species by Vega-Pérez & Bowman (1990). The new species is described and illustrated in detail in this paper.

Ctenocalanus heronae
Vega-Pérez & Bowman
Figs. 1–18

Ctenocalanus heronae Vega-Pérez & Bowman, 1990:100.

Material.—Brazil, Ubatuba region, São Paulo state, 23°58′S, 45°02′W, bottom depth 71 m, Dec 1987, collected from M/V *Almirante Saldanha* of the Instituto Oceanográfico, Universidade de São Paulo, sample 216T, closing net, mesh size 200 μm, vertical tow 65–20 m, temperature 15.05°C, salinity 35.48‰: ♀ holotype, Museu de Zoologia da Universidade de São Paulo (MZUSP 10,748), 50 ♀ paratypes (MZUSP 10,749); 8 ♀ paratypes, National Museum of Natural History, Smithsonian Institution (USNM 250958).

Diagnosis.—Female: Genital segment more expanded on left than on right side; in lateral view spermatheca extending dorsally to or beyond midheight of segment. First antenna reaching 4th urosomite, with complete suture between segments 9 and 10. Leg 4, exopod segment 1 with ctenospine with 0–4 teeth; segment 2 with ctenospine with 7 teeth; segment 3 ctenospines with 6–7 (proximal) and 7–9 (distal) teeth directed at angles of about 50° and 54° respectively to axis of segment.

Description of female.—Body length 1.23–1.32 mm, $\bar{X} = 1.27$ mm, $n = 50$. Rostrum with 2 slender filaments. Forehead moderately vaulted, convexly rounded in lateral view. Genital segment expanded laterally slightly more on left side than on right side; expanded ventrally at about midlength (Figs. 3, 4); spermatheca in form of band bending anteriad near base, extending to or beyond midheight of segment and slightly tapering; near posterior margin of genital segment on either side is a short row of delicate dorsolateral spinules.

Caudal rami with delicate hairs on medial margin, fewer on left ramus.

First antenna about 0.90 body length, reaching last urosomite, 24-segmented. Segments 9 and 10 separated by complete suture.

Second antenna (Fig. 6), coxa with 1 seta on distal medial margin. Basis with 2 medial setae. Endopod 2-segmented; 1st segment with 2 medial setae, 2nd segment with 6 setae on medial lobe and 8 setae on lateral lobe. Exopod 6-segmented, with incipient proximal and distal sutures on 2nd segment which bears 3 medial setae; 1st segment with 2 medial setae; segments 3–5 each with 1 medial seta; 6th segment with 1 medial and 3 terminal setae.

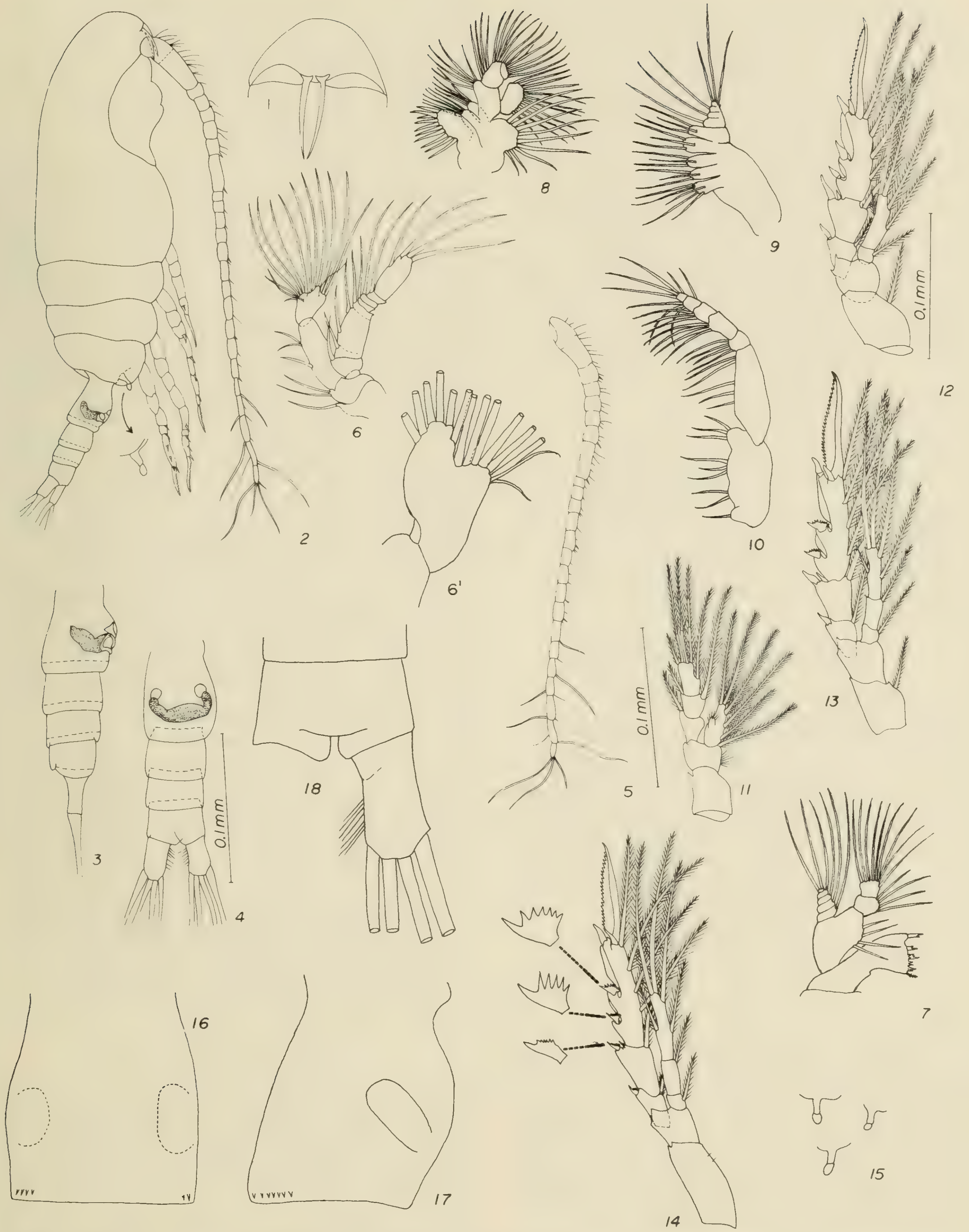
Mandible (Fig. 7), masticatory blade with 1 seta and 7 teeth bearing fragile hyaline cusps. Basis with 4 setae. Endopod 2-segmented; 1st segment with 4 setae, 2nd segment with 9 terminal setae. Exopod 5-segmented; 1st 4 segments each with 1 medial seta, 5th segment with 2 terminal setae.

First maxilla (Fig. 8), gnathobase with 9–10 spines; proximal and distal inner lobes with 5 and 4 setae respectively. Epipod with 7 long and 2 shorter setae. Endopod 2-segmented; 1st segment with 4 proximal and distal setae; 2nd segment with 7 terminal setae. Exopod with 11 setae.

Second maxilla (Fig. 9), 1st endite with 5 setae, 2nd–4th endites each with 3 setae. Endopod 5-segmented; 1st segment with 3 setae, 2nd, 3rd, and 4th segments each with 1 seta, 5th segment with 3 setae.

Maxilliped (Fig. 10) 7-segmented; 1st segment with 1 seta on proximal endite and 2, 3, and 3 setae on succeeding endites; 2nd segment with 3 setae near midlength and 2 near distal end.

Legs 1–4 (Figs. 11–14), segmentation and numbers of setae and spines identical to those of other species of *Ctenocalanus*. Leg 3 exopod 3rd segment, proximal and distal



Figs. 1–18. *Ctenocalanus heronae,* ♀. 1, Head and rostral filaments, ventral; 2, Habitus, lateral; 3, Urosome lateral; 4, Urosome, ventral; 5, Antenna 1; 6, Antenna 2; 6′, Antenna 2, distal segment of endopod; 7, Mandible; 8, Maxilla 1; 9, Maxilla 2; 10, Maxilliped; 11, Leg 1; 12, Leg 2; 13, Leg 3; 14, Leg 4; 15, Leg 5 from 3 different specimens; 16, Genital segment, dorsal; 17, Genital segment, lateral; 18, Anal segment and caudal rami, dorsal.

ctenoid spines respectively with 7 and 9 teeth and directed at angles of 67° and 65° to axis of segment. Leg 4 exopod, 1st segment lateral spine with 0–4 small teeth; 2nd segment lateral spine ctenoid, with 6 small teeth and large terminal tooth; 3rd segment, proximal and distal ctenoid spines respectively with 6–7 and 7–9 teeth and directed at angles of about 50° and 54° to axis of segment.

Left fifth leg (Fig. 15), biarticulate, proximal segment without articulation at base; distal segment short, round-oval to round, without the terminal point present in *C. vanus* and *C. tageae.*

Male.—Unknown.

Etymology.—Named for Gayle A. Heron, whose many contributions to the taxonomy of pelagic copepods include the description and illustrations of all the postnaupliar developmental stages of *Ctenocalanus citer.*

Comparisons and Discussion

Ctenocalanus heronae differs from *C. vanus* in having a more vaulted forehead and shorter 1st antennae. It differs from *C. citer* in the orientation of the ctenoid spines of the 4th leg which in *C. citer* are directed at only a small angle to the axis of the segment. It differs from *C. campaneri* in the shape of the genital segment and in having a complete suture between segments 9 and 10 of the 1st antenna. It differs from *C. tageae* in having a shorter 1st antenna and in the orientation of the ctenoid spines of the 4th leg; these spines are directed closer to the axis of the segment in *C. tageae.* Its spermatheca is similar in shape to that illustrated by Björnberg (1980, fig. 17) for her smaller form, but *C. heronae* has a shorter 1st antenna and a rather different shape of the genital segment.

As Almeida Prado-Por (1984) pointed out, the ctenoid spines are articulated at their bases. She concluded from this that they are movable and therefore their alignment in relation to the axis of the exopod is of no taxonomic importance. However, no muscles are attached to any of the spines, and the only movement they could undergo is an anterior–posterior flexion when the leg moves. We believe spine alignment is a valid taxonomic character.

Identification of the genus *Ctenocalanus* is simple because of the unique ctenoid spines on legs 3 and 4, as well as the reduced, uniramous ♀ leg 5. Identification to species can be difficult because specific differences are based on a limited number of rather subtle characters. The structure and orientation of the ctenoid spines of legs 3 and 4, the length of the 1st antenna in relation to the body length, the form of the genital segment and its spermatheca, and the degree of vaulting of the forehead have proved to be the most useful characters thus far. The present status of *Ctenocalanus* taxonomy is comparable to the formerly confused status of two other genera of Clausocalanidae, *Clausocalanus* and *Pseudocalanus,* before they were put in order by the fine revisionary monographs of Frost & Fleminger (1968) and Frost (1989), respectively. Even the identity of the type-species, *C. vanus* is uncertain. We do not know whether Giesbrecht's 1892 description and illustrations are based on his 1888 Pacific specimens or on the single female he had from the Gulf of Naples. If specimens from these two localities should prove to be specifically distinct, either the Gulf of Naples specimens or the Pacific specimens would have to be considered a new species.

Acknowledgments

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HYPHALION SAGAMIENSE, A NEW SPECIES OF CLAUSIDIIDAE (COPEPODA: POECILOSTOMATOIDA) ASSOCIATED WITH A VESICOMYID BIVALVE FROM THE HATSUSHIMA COLD-SEEP SITE IN SAGAMI BAY, JAPAN

Tatsuki Toda, Tomoyuki Miura, and Takahisa Nemoto

Abstract.—A new clausidiid copepod, *Hyphalion sagamiense,* found in association with a vesicomyid bivalve, *Calyptogena soyoae* Okutani, 1957, at a depth of 1170 m from the Hatsushima cold-seep site in Sagami Bay, Japan, is described. The species is morphologically very close to its only congener *Hyphalion captans* Humes, 1987 from Guaymas Basin, Gulf of California. The new copepod is distinguished from *H. captans* by the presence of 7-segmented first antenna, spinose paragnath, 5th leg with 2 broad segments, and in the male by a delicate seta on the long terminal claw of the 3-segmented maxilliped. Discovery of the present new species requires an amendment of the generic definition.

In recent years, a large number of new copepods have been described from deep-sea hydrothermal vents and cold-seep sites in the eastern Pacific and the Atlantic (Humes & Dojiri 1980a, 1980b; Fleminger 1983; Humes 1984, 1987, 1988a, 1988b, 1988c, 1988d, 1989a, 1989b, 1989c, 1989d). On the other hand, little is known of the copepods living at vents and/or seep sites in the western Pacific. The only work is one by Humes (1990) who described two new species from a deep-sea hydrothermal vent at the Mariana Back-Arc Basin.

A series of dives by the deep-sea submersible *Shinkai 2000* of the Japan Marine Science and Technology Center (JAMSTEC) have been made for multiple purposes at the Hatsushima cold-seep site which is characterized by the dominant occurrence of *Calyptogena soyoae* Okutani, 1957, since 1984 (Okutani & Egawa 1985). During Dive 315 of 1987, more than 40 specimens of this vesicomyid bivalve were collected and the animals associated with this mollusk were examined. A polychaete and a copepod species were found in the mantle cavity (Miura 1988), and the former was recently described (Miura & Laubier 1990). The purpose of this paper is to describe the parasitic copepod. The new copepod species is morphologically very close to *Hyphalion captans* Humes, 1987 collected from Guaymas Basin, Gulf of California; however, some unique characters in the new copepod support the establishment of a new taxon and require a minor emendation of the original diagnosis of the genus.

Materials and Methods

Calyptogena soyoae, hosts of the copepods, were collected during *Shinkai 2000* Dive 315 from the Hatsushima cold-seep site (depth 1170 m, 35°00.0′N and 139°13.8′E) in Sagami Bay, Japan, on 19 November 1987. Copepods were found on the gills of the bivalves and were collected using a small pipette with a tip diameter of 2.0–2.5 mm. Specimens were fixed in 10% formalin and preserved in 80% ethanol.

Copepods were dissected and examined in lactic acid under a stereo- and a compound microscope. Body length was measured from the anterior border of the prosome to the posterior edge of the caudal rami. Segment lengths were measured along the dorsal midline; widths were given as maxima unless otherwise stated. The segments of the first antenna were measured along their posterior, non-setose margins. All drawings were made with the aid of a camera lucida. The text abbreviations are: l = length, w = width, P1–P4 = leg 1–leg 4, exp = exopod, and enp = endopod. In the armature formulae of legs 1–4, Roman and Arabic numerals caps represent spines and setae, respectively.

Family Clausidiidae Embleton, 1901
Genus *Hyphalion* Humes, 1987
Hyphalion sagamiense, new species
Figs. 1–4

Material examined.—40 ovigerous females, 2 males, 1 copepodite. Types deposited in National Science Museum (NSMT), Tokyo, Japan. Holotype female, NSMT-Cr 10159; allotype male, NSMT-Cr 10160; paratype 34 females, NSMT-Cr 10161. Additional materials deposited in Plankton Division, Ocean Research Institute, University of Tokyo and Faculty of Fisheries, Kagoshima University.

Habitat.—Gills of *Calyptogena soyoae* Okutani, 1957.

Locality.—Hatsushima cold-seep site, Sagami Bay, Japan.

Description–Female.—Body (Fig. 1a, b) elongate, flattened; body surface smooth. Total length 2.01 mm, greatest width 0.63 mm. Greatest dorsoventral thickness 0.28 mm. Length ratio of prosome to urosome 1.21:1.

Prosome consisting of 4 somites. Ratio of length to width of prosome 1.69:1. Somite bearing leg 1 fused with cephalosome; cephalothorax 532 × 628 μm (l × w). Somites bearing legs 2, 3, and 4 decreasing in width posteriorly: 161 × 544, 188 × 466, 140 × 388 μm (l × w). Epimeral areas of pedigerous somites rounded.

Urosome with 4 somites. Somite bearing leg 5 (Fig. 1c) 112 × 321 μm (l × w). Genital somite, much broader than long in dorsal view 180 × 312 μm (l × w); its lateral margins expanded. Genital areas located dorsolaterally on expanded portions of somite (Fig. 1d); each area with 2 small smooth setae, 24 μm and 26 μm. Four abdominal somites: 154 × 231, 112 × 199, 96 × 157, and 81 × 151 μm (l × w). Anal somite (Fig. 1e) with 4 broad anteroventral striated scales from right to left 15 × 10, 15 × 13, 16 × 12, 17 × 15 μm (l × w); each posteroventral corner (Fig. 1f) with a single row of spinules.

Caudal ramus (Fig. 1c) longer than wide, 184 × 65 μm (l × w), ratio of length to width 2.83:1. Ramus armed with 6 setae: outer lateral seta 43 μm; dorsal seta 67 μm; innermost terminal seta 82 μm; two long median terminal setae 207 μm (outer) and 395 μm (inner); all these setae smooth. Outermost terminal seta minutely barbed and 111 μm.

Egg sac containing 2 eggs (Fig. 1g). Egg approximately 280 × 250 μm (4 eggs measured).

Rostrum (Fig. 2a) broad, posterior margin rounded without ornamentation. First antenna (Fig. 2b) 7-segmented. Length of each segment: 57, 74, 31, 43, 26, 29, and 43 μm, with formula for armature: 5, 15, 6, 3, 5, 2 + 1 aesthete, and 7 + 1 aesthete, respectively. All setae smooth except some of those on segments 4–7 with minute barbules. Second antenna (Fig. 2c) 3-segmented. First and second segments with single seta. Third segment recurved, with 3 inner subterminal setae, 1 inner terminal seta, 1 outer terminal seta and 3 very long, recurved, sickle-shaped, terminal claws, longest 228 μm. All setae and claws smooth. Claws of both sides forming a strong prehensile structure.

Labrum (Fig. 2d) broad, 59 × 106 μm (l

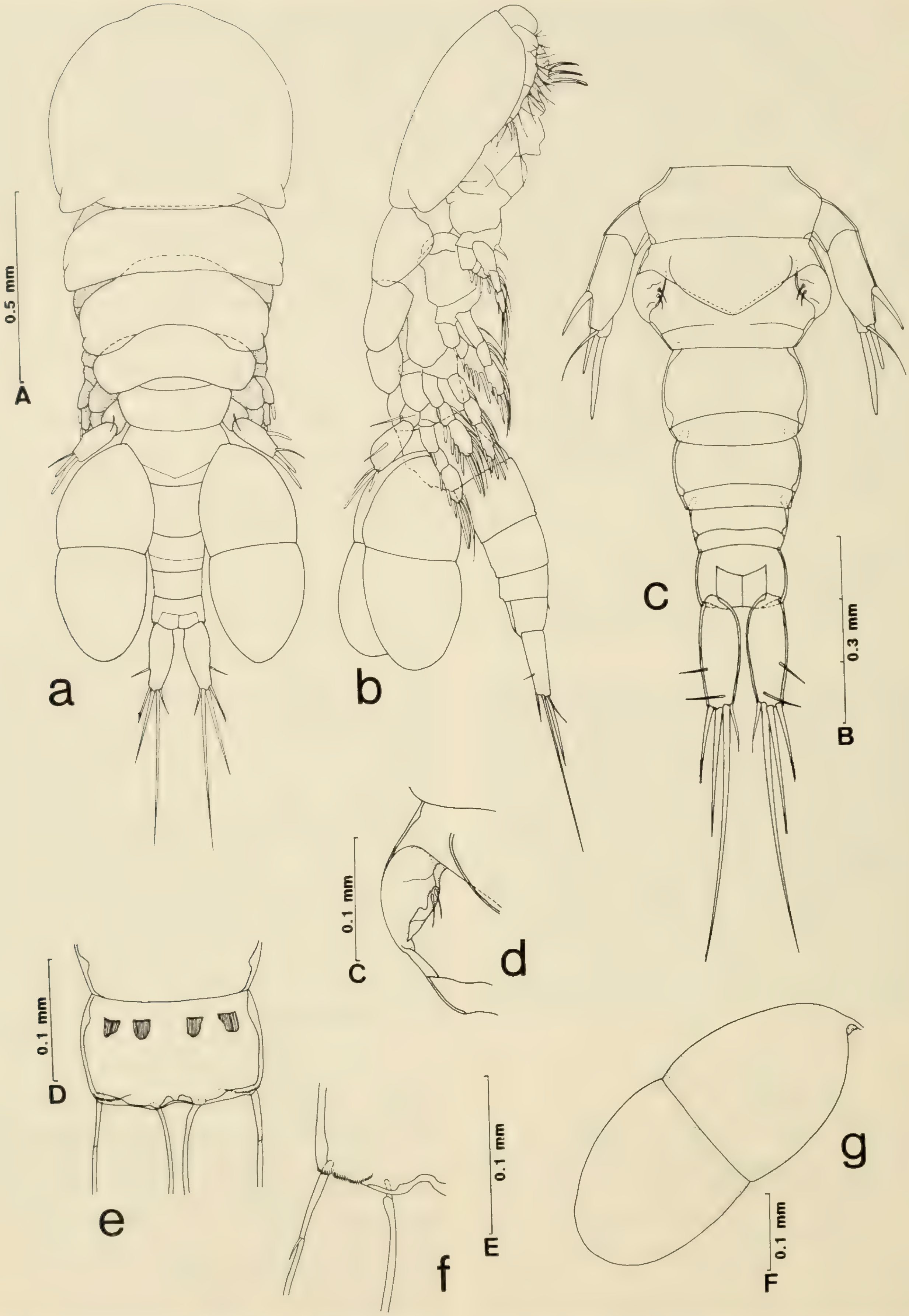

Fig. 1. *Hyphalion sagamiense,* new species. Female: a, dorsal (scale A); b, lateral (A); c, urosome, dorsal (B); d, genital area, dorsal (C); e, anal segment, ventral (D); f, right side of anal segment, ventral (E); g, egg sac, dorsal (F).

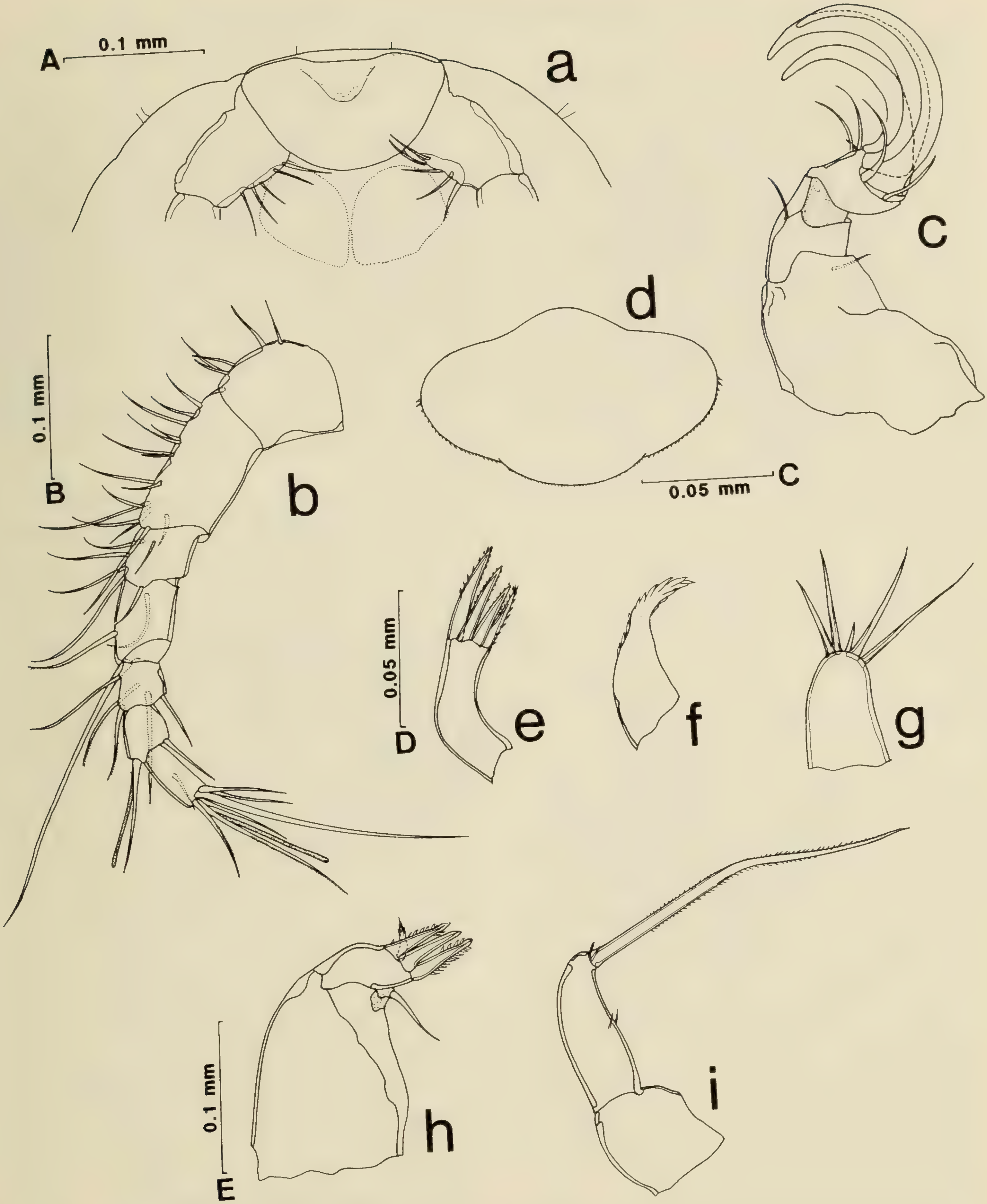

Fig. 2. *Hyphalion sagamiense,* new species. Female: a, rostral area, ventral (scale A); b, first antenna, dorsal (B); c, second antenna (B); d, labrum, ventral (C); e, mandible (D); f, paragnath (D); g, first maxilla (D); h, second maxilla (E); i, maxilliped (E).

× w), with posteroventral rounded margin bearing small spinules.

Mandible (Fig. 2e) flexed, bearing 4 barbed spines terminally. Paragnath (Fig. 2f) falciform with denticulated terminal part. First maxilla (Fig. 2g) digitiform with 5 smooth setae: 4 long setae and 1 middle short seta. Second maxilla (Fig. 2h) 2-segmented. First segment massive with 1 delicate seta. Second segment smaller with 3 spinulose spines, and 1 haired seta. Maxilliped (Fig. 2i) 2-segmented. First segment unarmed. Second segment with 2 very small inner setae, 2 small terminal setules and 1 very long prominent barbed seta. Last seta slightly bent beyond midlength, 228 μm.

Legs 1–4 (Fig. 3a–d) biramous with 3-segmented rami. Armature as follows:

P1	coxa 0-1	basis 1-I	exp I-0; I-1; III, I, 4
			enp 0-1; 0-1; I, 5
P2	coxa 0-1	basis 1-0	exp I-0; I-1; III, I, 5
			enp 0-1; 0-2; II, I, 3
P3	coxa 0-1	basis 1-0	exp I-0; I-1; III, I, 5
			enp 0-1; 0-2; II, II, 2
P4	coxa 0-1	basis 1-0	exp I-0; I-1; II, I, 5
			enp 0-1; 0-2; I, III, 1

Intercoxal plate of leg 1 smooth, those of legs 2–4 with small spinules on surface. Inner seta on coxa of all 4 legs sword-shaped and haired. Inner spine on basis of leg 1 stout and minutely barbed 56 μm long. Leg 5 (Fig. 3e) 2-segmented. First segment 78 × 75 μm, with a single dorsal seta 90 μm. Second segment 113 × 82 μm, ratio 1.38:1, with outer marginal spine 75 μm, subterminal spine 77 μm, terminal spine 131 μm and terminal seta 81 μm. All 3 spines barbed, seta smooth. Leg 6 probably represented by presence of 2 setae in genital area (Fig. 1c, d).

Color of living specimens red.

Male.—General form (Fig. 4a) similar to that of female. Total length 1.42 mm, greatest width 0.47 mm, and greatest dorsoventral thickness 0.23 mm. Length ratio of prosome to urosome 1.30:1.

Prosome consisting of 4 somites. Ratio of length to width of prosome 1.90:1. Cephalothorax 445 × 465 μm (l × w). Somites with legs 2, 3, and 4: 147 × 398, 145 × 330, 89 × 260 μm (l × w).

Urosome with 5 somites, less than in female. Somite bearing leg 5 51 × 167 μm. Genital somite longer than wide, 204 × 174 μm. Posteroventral lappets (Fig. 4b) on genital somite semicircular, not prominent. Lappet with 1 seta minutely barbed, 66 μm. Three postgenital somites from anterior to posterior 137 × 156, 110 × 129, and 88 × 105 μm (l × w). Anal somite with 4 ventral scales as in female.

Caudal ramus similar to that of female, but slightly shorter in male, 134 × 47 μm, ratio 2.85:1.

Rostrum, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla like those of female. First antenna (Fig. 4c) 7-segmented. Length of each segment: 36, 63, 33, 38, 20, 25, and 39 μm, with formula or armature: 5, 15, 6, 4, 5, 2 + 1 aesthete, and 7 + 1 aesthete, respectively. Maxilliped (Fig. 4d) 3-segmented (assuming claw to represent third segment). First segment with 1 inner smooth seta. Large triangular second segment with inner surface having 1 small setae, and 2 rows of spines (Fig. 4e). Claw (Fig. 4d, e) recurved, 149 μm, bearing 2 unequal, proximal, smooth setae, and 1 delicate setiform sensory organ, attached to terminal part of claw.

Legs 1–4 as in female. Leg 5 (Fig. 4f) similar to that of female. First segment 65 × 53 μm, with dorsal seta 65 μm. Second segment more slender than in female, 91 × 48 μm, ratio 1.90:1, outer marginal spine 56 μm, subterminal spine 55 μm, terminal spine 105 μm, and seta 71 μm. Leg 6 (Fig. 4b) consisting of posteroventral flap on genital segment with 1 pinnate seta.

Color of living specimens red.

Etymology.—This species has been named after its sampling site, Sagami Bay.

Remarks.—Several features of the new species conform to the genus *Hyphalion* Humes, 1987: the habitus, the urosome with

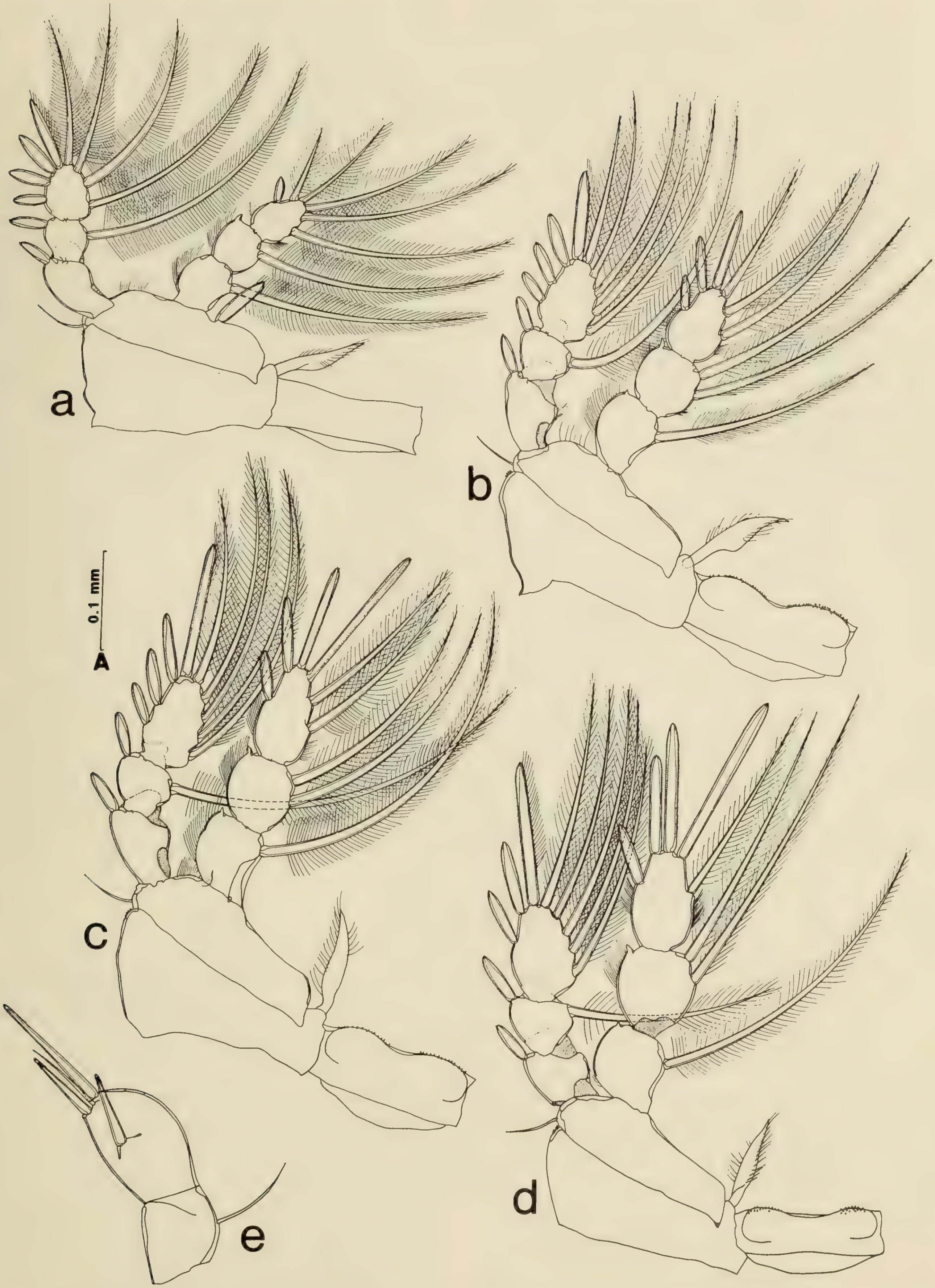

Fig. 3. *Hyphalion sagamiense,* new species. Female: a, leg 1 and intercoxal plate, anterior (scale A); b, leg 2 and intercoxal plate, anterior (A); c, leg 3 and intercoxal plate, anterior (A); d, leg 4 and intercoxal plate, anterior; e, leg 5, left, anterior (A).

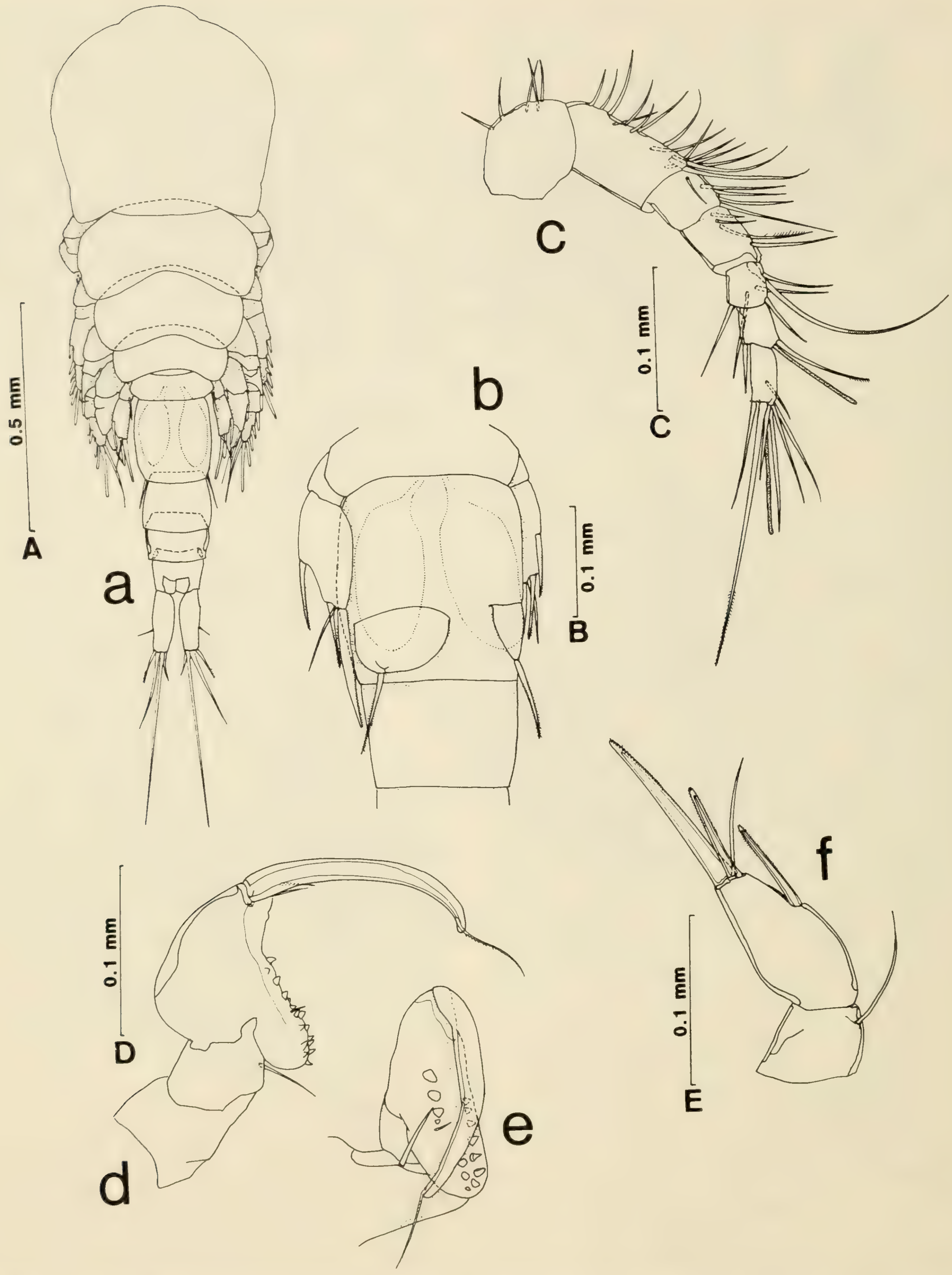

Fig. 4. *Hyphalion sagamiense,* new species. Male: a, dorsal (scale A); b, genital segment, legs 5 and 6, ventrolateral (B); c, first antenna (C); d and e, maxilliped (D); f, leg 5, dorsal (E).

6 somites in the female and 5 in the male, the 3-segmented prehensile second antenna with 3 strongly recurved claws, the mandible with 4 elements, the first maxilla with 5 setae, the 2-segmented second maxilla consisting of a large first segment with 1 seta and small second segment with 3 spines and 1 seta, the 2-segmented maxilliped of the female with the second segment having an extremely long seta, and the spinal and setal formulae on legs 1–5. However, *Hyphalion sagamiense* may be distinguished from its only congener, *H. captans* by the following characters: (1) The first antenna is 7-segmented; the third segment of *H. captans* corresponds to third and fourth segments of *H. sagamiense,* judging from the proportions and the ornamentation; (2) the tapering paragnath has a spinose tip; (3) the second segment of leg 5 is broad, and the length to width ratio is 1.38:1 in the female and 1.90:1 in the male, but in *H. captans,* 2.23:1 and 2.43:1, respectively; (4) the length to width ratios of the caudal rami are 2.83:1 and 2.85:1 in female and male, respectively, but in *H. captans* 3.17:1 and 3.15:1; (5) the male maxilliped is 3-segmented; (6) the long terminal claw of the male maxilliped has a delicate apical seta presumed to be a sensory organ.

Discussion

Hyphalion sagamiense is the first copepod described from deep-sea cold-seep sites in the western Pacific. On the other hand, its only congener *Hyphalion captans* was collected from Guaymas Basin, Gulf of California. Although these two copepods occurred separately on either side of the Pacific Ocean, they are very similar in several features such as body form, second antenna, mandible, first maxilla, second maxilla, and maxilliped. Additionally, the spinal and setal formulae on legs 1–5 in *H. captans* and *H. sagamiense* are the same; consequently, these two species are considered to be closely allied. The discovery of the new species validated the original establishment of the genus *Hyphalion* proposed by Humes (1984) for the type-species *H. captans,* and helped to more clearly define the genus. The generic definition was partially emended in order to accommodate the new species. The presence of the 7-segmented first antenna and the 4-segmented maxilliped of the male was added to the original generic diagnosis.

The family Clausidiidae currently consists of nine genera included by Vervoort & Ramirez (1966) and three genera proposed afterwards: *Clausidium* Kossmann, 1874, *Conchyliurus* Bocquet & Stock, 1957a, *Cotylomolgus* Humes & Ho, 1967, *Giardella* Canu, 1888, *Hemicyclops* Boeck, 1873, *Hersiliodes* Canu, 1888, *Hippomolgus* Sars, 1917, *Hyphalion* Humes, 1987, *Leptinogaster* Pelseneer, 1929, *Myzomolgus* Bocquet & Stock, 1957b, *Pseudopsyllus* T. Scott, 1902, and *Tychidion* Humes, 1973. Presently, among these genera, *Hyphalion* is considered most closely related to *Hemicyclops.* The 7-segmented first antenna of the new species conforms to the character of *Hemicyclops* (6-segmented in the type-species of *Hyphalion*). The minor emendation of the generic definition, therefore, makes the distinction between the two genera a little obscure. However, both species of the genus *Hyphalion* can still be distinguished from *Hemicyclops* and the other genera in the family Clausidiidae by the unusual armature of the second antenna.

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GRUBEOSYLLIS CELIAE, A NEW SPECIES OF EXOGONINAE (SYLLIDAE: POLYCHAETA) FROM OFF CEUTA, SPAIN

Julio Parapar and Guillermo San Martín

Abstract.—*Grubeosyllis celiae* (Exogoninae; Syllidae; Polychaeta) from sandy bottoms off Ceuta, a Spanish city on the Mediterranean coast of Africa, is described. The new species is characterized by unusual dorsal cirri, the shape of its compound setae, and its unidentate capillary dorsal simple setae.

We studied the polychaetes from samples of sublittoral sand, taken by scuba diving during the summer of 1986 in an expedition carried out by the Musee d'Histoire Naturelle de Paris (Ceuta-86). Provisionally, 88 species have been identified, including a new species of *Exogone,* described by San Martín & Parapar (1990).

In this report, a new species of *Grubeosyllis* Verrill, 1900 is described. The specimens have been mounted in slide preparations using glycerine jelly. Observations and measurements were made by means of a microscope provided with interference contrast optics (Nomarsky). Drawings were made by using a drawing tube. All measurements were taken excluding appendages and setae. The type material is deposited in the Museo de Historia Natural Luis Iglesias de la Universidad de Santiago de Compostela (MHNS-2-Pol 1-6), Spain.

Family Syllidae Grube, 1850
Subfamily Exogoninae Rioja, 1925
Genus *Grubeosyllis* Verrill, 1900

Grubeosyllis celiae, new species
Fig. 1

Material examined.—Playa Benitez, Ceuta (Spain) (36°54′15″N, 5°19′54″W); sand; 23 m; holotype and 5 paratypes. El Pineo, Ceuta (Spain) (36°52′36″N, 5°19′46″W); sand; 11 m; 2 paratypes. Holotype and paratypes under the same catalog number: MHNS-2-Pol.

Etymology.—The species is named in honor of Dr. Celia Besteiro, Departamento de Bioloxía Animal, Universidade de Santiago de Compostela (Spain), for her help and friendship.

Description.—All specimens incomplete; similar in size. Body moderately long, slender. Holotype, a mature female, is nearly 3 mm long, 0.2 mm wide, with 30 setigers. Prostomium pentagonal to ovate (Fig. 1A). Four large, red eyes, one pair slightly in front of other pair. Median antenna fusiform or club-shaped, originating on middle of prostomium, similar in length to prostomium and palps together. Lateral antennae similar, but slightly shorter, originating near anterior margin of prostomium. Palps shorter than prostomium, broad, fused along their length; sometimes showing a faint line of fusion. Tentacular cirri similar both in shape and length to antennae (Fig. 1A); those of dorsal pair longer than those of ventral pair. Dorsal cirri on all setigers, cylindrical to club-shaped; bases slender and usually distal end thicker. Dorsal cirri fragile, longer than parapodial lobes, usually shorter than setae, except anteriorly. Compound setae (Fig. 1B) similar on all parapodia, without distinct antero-posterior gradation in shape or in length; blades slender, strongly bidentate, with distal and proximal teeth well sep-

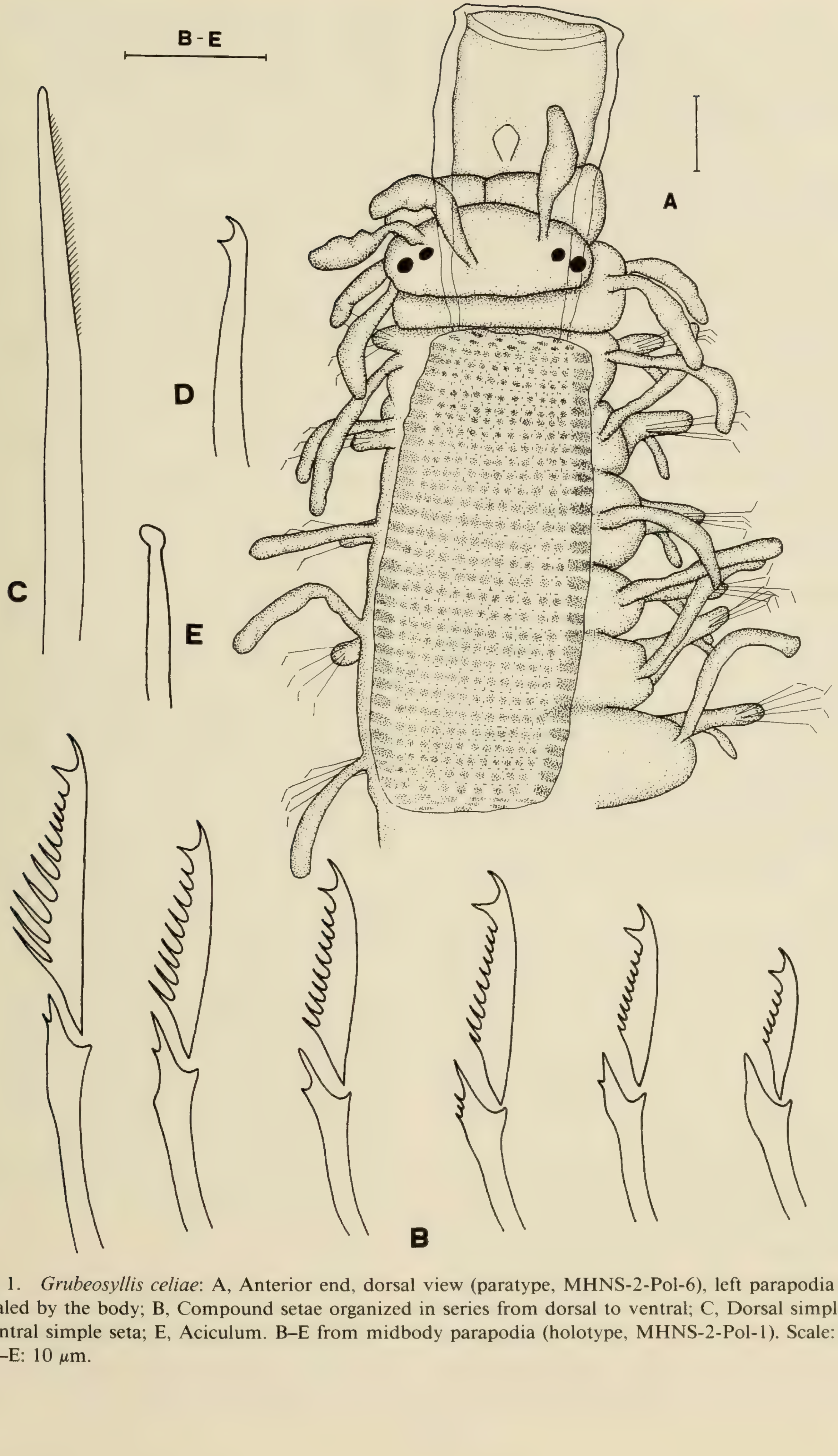

Fig. 1. *Grubeosyllis celiae*: A, Anterior end, dorsal view (paratype, MHNS-2-Pol-6), left parapodia partly concealed by the body; B, Compound setae organized in series from dorsal to ventral; C, Dorsal simple seta; D, Ventral simple seta; E, Aciculum. B–E from midbody parapodia (holotype, MHNS-2-Pol-1). Scale: A, 64 μm. B–E: 10 μm.

arated, forming almost a right angle, distal tooth somewhat curved, proximal tooth slightly thicker than distal one; blades provided with long, thin serrations on cutting margin. Slight dorso-ventral gradation present, ventral blades shorter, with shorter spines on cutting margin. A parapodium of midbody with about 9 setae, with blades 23 μm above, 10 μm below. Solitary dorsal simple seta (Fig. 1C) from first setiger, straight, unidentate, provided with short, dense serrations on ventral side, thin anteriorly increasing in thickness posteriorly. Solitary ventral simple seta from midbody, bidentate with similar teeth to blades of compound setae, s-shaped, smooth (Fig. 1D). Solitary acicula in each parapodium, slender, with rounded tip, increasing in thickness posteriorly (Fig. 1E). Pharynx long and wide, partial or totally everted on all specimens, anterior rim smooth; pharyngeal tooth rhomboidal, placed in front of midline of pharynx. Proventriculus massive, barrel shaped, longer than pharynx, extending through about 6 segments, with about 34 muscle cell rows. Visible pharynx to proventricle length ratio between 0.62 and 0.72. Length to width ratio of proventricle between 2.30 and 2.50.

Holotype and one paratype mature females, with 1–2 oocytes in each segment of midbody.

Remarks.—*Grubeosyllis* was described by Verrill (1900), but it was considered a synonym of *Brania* Quatrefages, 1865 by Hartman (1959).

San Martín (1984) described a new genus, *Pseudobrania,* for a group of species of *Brania*; however San Martín (1991) referred this genus to *Grubeosyllis.* The distinction between *Grubeosyllis* and *Brania* as currently defined is here considered valid.

Most of the species of *Grubeosyllis* have fusiform dorsal cirri, with bulbous bases and long, pointed tips, as in *G. clavata* (Claparède, 1863) (see Fauvel 1923:296, San Martín 1984:167); *G. clavata* (Claparède, 1863) (see Fauvel 1923:298, San Martín 1984:164); *G. subterranea* (Hartmann-Schröder, 1956:89) (see Westheide 1974:87, Campoy 1982:256); *G. concinna* (Westheide, 1974:91); *G. vieitezi* (San Martín, 1984:160); *G. alvaradoi* (San Martín, 1984: 152); *G. yraidae* (San Martín, 1984:156); *G. nitidula* Verrill, 1900:628 (see San Martín 1991); *G. euritmica* (Sardá, 1984:10); *G. balani* (Hartmann-Schöder, 1960:102) (see Alós et al. 1983:292); *G. opisthodentata* (Hartmann-Schröder, 1979:101); *G. gracilis* (Hartmann-Schröder, 1960:101); *G. longisetosa* (Hartmann-Schröder, 1979:102), and *G. brevipharyngea* (Banse, 1972:198).

The remaining species of *Grubeosyllis,* have cylindrical dorsal cirri, similar to those in *G. celiae,* but have very different compound setae: *G. mediodentata* (Westheide, 1974:93); *G. swedmarki* (Gidholm, 1962: 256) (see Campoy 1982:251), and *G. rugulosa* Verrill, 1900:629 (see San Martín 1991).

Grubeosyllis rugulosa Verrill, 1900 appears to be the most closely related species; this species has a very similar body, however it has strongly bidentate dorsal simple setae and in the blades of the compound setae the gap between the teeth is far less prominent.

Although the dorsal cirri and setae of the new species are unusual within the genus, the pharynx, pharyngeal tooth, and proventriculus are typical of *Grubeosyllis.* We therefore place this species in *Grubeosyllis* instead of describe a new one. The genus *Psammosyllis* Westheide, 1990, with the only known species *P. aliciae* (Westheide, 1990:165) has similar dorsal cirri, pharynx and proventriculus. However, *P. aliciae* has very long, completely fused palps, the pharyngeal tooth is not rhomboidal and it is located behind the midline of the pharynx. Apparently, *Psammosyllis* is a very close genus to *Grubeosyllis.*

Acknowledgments

We wish to express our gratitude to Drs. Victoriano Urgorri and Jesus S. Troncoso, Departamento de Bioloxía Animal, Universidade de Santiago de Compostela, Spain, who provided us with the samples in which the specimens of this new species were found.

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ON THE SYSTEMATIC POSITION OF *MONROIKA AFRICANA* (MONRO) (POLYCHAETA: SABELLIDAE: FABRICIINAE) AND A DESCRIPTION OF A NEW FABRICIIN GENUS AND SPECIES FROM AUSTRALIA

Kirk Fitzhugh

Abstract.—The definition of the monotypic sabellid polychaete genus *Monroika* Hartman is emended based on additions to the description of the type species, *Manayunkia africana* Monro. Although type and nontype material is poorly preserved, the branchial crown appears to have a construction like that of some *Manayunkia* species. A cladistic analysis of fabriciin taxa (sensu Fitzhugh) places *M. africana* either as a sister group to, or as a species within *Manayunkia*. Potential systematic consequences of these results are discussed. A new genus and species from Australia, *Parafabricia ventricingulata,* is described, which is a sister taxon to *Augeneriella* Banse and *Fabricinuda* Fitzhugh.

The sabellid polychaete *Manayunkia africana* Monro, 1939 is a small, tubicolous, freshwater species known only from Matadi, Democratic Republic of the Congo, approximately 150 km upstream from the mouth of the Congo River. The species is described by Monro (1939:220) as living in swift water, forming "... incrustations composed of clusters of small intertwining sandy tubules" on the shells of the freshwater gastropod, *Hydrobia plena,* as well as on stones. Whereas Monro apparently examined specimens only found on *H. plena,* he attributed to *M. africana* some dried tubes encrusted on a stone from the M'Pozo River, upriver from Matadi.

Monro's placement of this polychaete species in *Manayunkia* rested on the reported presence of near-"spatulate" thoracic notosetae (=pseudospatulate setae sensu Fitzhugh 1989, see below) in some other species of *Manayunkia. Manayunkia africana* is said to have "spatulate" setae in setigers 2–5. Monro did not comment on the rarely described (e.g., Zenkevitsch 1925: fig. Gh, i) occurrence of this setal form in *Fabricia stellaris* [Müller; =*F. sabella* (Ehrenberg), see Fitzhugh 1990d].

Monro (1939:220) reported that the state of preservation of specimens is poor, such that "delicate parts such as the gills are partly disintegrated." Thus, his illustration (Monro 1939:fig. 1) of the branchial crown is not very informative. Monro did, however, describe the branchial crown as being composed of about 12 "filaments" (=radioles), lacking "barbules" (=pinnules), which are joined by a "high palmer membrane." The opinion that the branchial crown of *Manayunkia* species lacks pinnules (="barbules") has been a common misconception (e.g., Southern 1921, Friedrich 1939, Hartman 1951; but see, however, Zenkevitsch 1925, Pettibone 1953:fig. 1C, D).

In a review of fabriciin taxa (sensu Rioja 1923), Hartman (1951) proposed the new genus *Monroika* to accommodate *Manayunkia africana.* Hartman's basis for this change rested solely on Monro's (1939) description of the putative unique combination of numerous nonpinnulate radioles and a palmate membrane. Hartman thus considered *Monroika* similar to *Manayunkia* on the common (though erroneous) assumption that all species in both genera have nonpinnulate radioles (see below).

The most thorough description of *Monroika africana* is given by Jones (1974) based on the type material. While Jones provided excellent illustrations of all setal forms, drawings of the body (Jones 1974:fig. 1) are incomplete insofar as the branchial crown is not shown and is not described. While Jones (1974:219) supported Hartman's (1951) decision to erect *Monroika,* he considered the "type and distribution of setae and the number of thoracic and abdominal setigers" to be the "crucial generic differences between *Monroika* and *Manayunkia* . . ." as opposed to the questionable presence of a palmate membrane.

This paper is a partial emendation of the definition of *Monroika* based on type and nontype material of *Manayunkia africana.* A new fabriciin (sensu Fitzhugh 1989, 1991a) genus and species from Australia, *Parafabricia ventricingulata,* is also described. The cladistic relationships and status of *Monroika* and *Parafabricia* are then examined in relation to other fabriciin genera and species. Morphological terms used here follow from definitions given by Fitzhugh (1989) and their subsequent application by Fitzhugh (1990a, 1990b, 1990c, 1990d, 1990e, 1991a).

Specimens examined are deposited in one of the following institutions: Allan Hancock Foundation Collection of the Los Angeles County Museum of Natural History (LACM-AHF), British Natural History Museum (BMNH), U.S. National Museum of Natural History, Smithsonian Institution (USNM), and the Australian Museum, Sydney (AM).

Monroika Hartman, 1951, emended

Monroika Hartman, 1951:389; 1959:551 [list].—Jones, 1974:218–219.—Fauchald, 1977:139.

Type species.—*Manayunkia africana* Monro, 1939, by monotypy.

Diagnosis.—Fabriciin species with 8 thoracic and 2 abdominal setigers. Branchial crown with 2 pairs of radioles; all pinnules arranged in pectinate fashion except for unpaired proximalmost pinnule of first radiole being displaced and adjacent to dorsal lips. Dorsal lips erect, broadly rounded. Presence or absence of ventral lips unknown. Pair of vascularized, filamentous appendages present. Branchial hearts (?) poorly developed. Branchial lobes not fused middorsally. Branchial skeleton absent. Anterior peristomial ring developed as a membranous collar; narrowly separated middorsally. Posterior peristomial ring collar absent. Peristomial and pygidial eyes absent. Superior thoracic notosetae elongate, narrowly hooded. Inferior thoracic notosetae of setigers 1–2 and 6–8 short forms of elongate, narrowly hooded; setigers 3–5 pseudospatulate. Thoracic uncini acicular; large tooth above main fang; hood present. Abdominal uncini rasp-shaped plates; manubrium about same length as dentate region; dentate region with several teeth per row. Abdominal neurosetae modified, elongate narrowly hooded.

Remarks.—The present diagnosis is consistent with that given by Jones (1974) except that the distribution of pseudospatulate setae is limited to setigers 3–5 as opposed to 2–5. While inferior thoracic notosetae in setiger 2 are short forms of the elongate, narrowly hooded condition of superior thoracic notosetae, the former are slightly shorter than the inferior thoracic notosetae in setigers 6–8 and the proximal region of the hood is slightly wider. As a result, inferior thoracic notosetae of setiger 2 can have an almost intermediate appearance to inferior elongate, narrowly hooded and pseudospatulate forms. A similar phenomenon has been noted by Banse (1956) in species of *Fabricia* Blainville, 1828.

The branchial crown appears to show a pattern of construction identical to that of several *Manayunkia* species, e.g., *M. speciosa* Leidy, 1859 and *M. baicalensis* (Nusbaum, 1901), in that pinnules extend from the radioles in a pectinate arrangement (see cladistic analysis below; Fig. 4A). In addition to there being only two pairs of radioles, a pair of dorsal lips, and a pair of vascularized, ventral filamentous appendages, there also are a pair of slender, unbranched appendages just dorsal to the dorsalmost radioles and which are continuous with the dorsal lips (cf. Fig. 4A, B). These appendages are referred to here as displaced pinnules and are the same as what Zenkevitsch (1925:fig. D) called dorsal lips (*Dorsallippenauswüchse*) in *M. baicalensis* and what Pettibone (1953:fig. 1D) referred to as mediodorsal tentacles in *M. speciosa.* Banse (1956:425–426) suggested these appendages in *Manayunkia* are homologous to pinnules of the dorsalmost radioles, having migrated to a more proximal position on the radiole. Fitzhugh (1989:63) noted, however, that in *M. speciosa* the side from which pinnules extend from the dorsalmost radioles is ventral to this structure (Fig. 4A). Additional aspects of the displaced pinnules in *Manayunkia* and *Monroika* are discussed in the cladistic analysis below.

Monroika africana (Monro, 1939)

Manayunkia africana Monro, 1939:220–223, figs. 1–5.—Wesenberg-Lund, 1958: 29 [list].

Monroika africana.—Hartman, 1951:389–390; 1959:551 [list].—Jones, 1974:219–221, figs. 1, 2, table 1.—Fauchald, 1977: 139 [list].

Material examined.—Democratic Republic of the Congo, Congo River at Matadi, E. Dartevelle, coll. Syntypes: 1 incomplete specimen mounted on microscope slide (BMNH 1939.7.17.1); 3 incomplete specimens mounted on microscope slide (BMNH 1939.7.17.2). Additional material: several incomplete specimens mounted on slide (USNM 50913); several complete specimens from sandy tubes on two *Hydrobia plena* shells (BMNH ZK 1939.7.17.13–14).

Description.—All specimens in very poor, degraded condition. Branchial crown comprising about one-fifth of total body length. Two pairs of radioles, each with 3–5 pairs of pinnules; all pinnules terminate at about same height. A pair of displaced pinnules present between dorsal midline and dorsalmost radiole pair; terminate at same height as pinnules. Displaced pinnules lead to pair of low dorsal lips. Vascularized ventral filamentous appendages present, same height as radioles. Branchial hearts present, poorly developed. Membranous, anterior peristomial ring collar highest ventrally, broadly rounded; very shallow laterally then slightly higher dorsolaterally; dorsolateral margins with pair of narrow, shallow notches; completely separated middorsally by narrow gap. Demarcation between anterior and posterior peristomial rings not visible. Tubes about 2 times longer than animals, composed of quartz sand grains and some detritus; very firm. No brooding observed.

Remarks.—Setal counts can be found in Jones (1974:tables 1, 2), with the exception that what he described as "spatulate" setae in setiger 2 are here called short forms of elongate, narrowly hooded setae (see Remarks above). All features described here are illustrated by Jones with the exception of the branchial crown.

Discerning specific structures on the branchial crown is extremely difficult. For example, establishing the pattern of pinnule branching, the presence of displaced pinnules, and presence of ventral filamentous appendages is only possible by way of tracing what appear to be blood vessels and musculature. As a result, I am not wholly confident of my interpretation of branchial crown structures. Some implications of these limitations are discussed below as part of the cladistic analysis.

Parafabricia, new genus

Type species.—*Parafabricia ventricingulata,* new species.

Etymology.—The genus name is derived from its inferred close relationship and appearance to *Fabricia.*

Diagnosis.—Fabriciin species with 8 thoracic and 3 abdominal setigers. Branchial crown with 3 pairs of radioles, pinnules arranged in pectinate fashion. Dorsal lips triangular. Ventral lips and ventral filamentous appendages absent. Branchial hearts present. Branchial lobes not fused middorsally. Branchial skeleton absent. Anterior peristomial ring margin developed ventrally as broad, distally rounded lobe, laterally and dorsally as rounded shelf; dorsolateral, lateral and portion of ventral areas of ring concealed by posterior peristomial ring. Posterior peristomial ring distinctly wider than long. Posterior peristomial ring collar absent. Peristomial and pygidial eyes present. Transverse "glandular" ridge present on ventrum of setiger 5. Superior thoracic notosetae elongate, narrowly hooded. Inferior thoracic notosetae of setigers 2 and 8 short forms of elongate, narrowly hooded state; setigers 3–7 pseudospatulate. Thoracic uncini acicular; large tooth above main fang; hood present. Abdominal uncini rasp-shaped plates; manubrium about same length as dentate region; dentate region with several teeth per row. Abdominal neurosetae modified, elongate narrowly hooded. Body wall pigmentation usually restricted to branchial crown and thoracic region; light to dark brown; well to poorly developed.

Remarks.—*Parafabricia* is the sister group to *Augeneriella* Banse, 1957 and *Fabricinuda* Fitzhugh, 1990c (see cladistic analysis below); the sister group to this clade is *Fabricia. Parafabricia* closely resembles both *Fabricia* and *Augeneriella* in development of the ventral lobe of the anterior peristomial ring and the distribution of thoracic inferior pseudospatulate setae in setigers 3–7. The short manubrium state in abdominal uncini distinguishes *Parafabricia* from *Fabricia* (see also Banse 1956; Fitzhugh 1989, 1990d), whereas *Augeneriella* has branched, vascularized, ventral filamentous appendages. *Fabricinuda* has pseudospatulate setae in setigers 3–8 and lacks the ventral lobe extension of the anterior peristomial ring.

The most distinctive features of *Parafabricia* include 1) partial extension of the posterior peristomial ring segment over the anterior ring, resulting in an obvious mid-dorsal gap in the posterior ring, and 2) the ventral "glandular" ridge on setiger 5. This ridge closely resembles the "glandular girdle" encircling setiger 2 of some plesiomorphic sabellin genera (sensu Fitzhugh 1989, 1991a), e.g., *Desdemona* Banse, *Oriopsis* Caullery & Mesnil, *Chone* Krøyer, and *Jasmineira* Langerhans. Aspects of this ridge are discussed below in the Remarks on *P. ventricingulata.*

Parafabricia ventricingulata, new species
Figs. 1–3

Material examined.—Australia, Queensland, Great Barrier Reef, upper reef crest on northeastern side of One Tree Reef, 23°30′S, 152°05′E, in intertidal mats of green alga *Boodlia composita,* 6 Dec 1987, coll. G. Rouse. Holotype (AM W 20717). Paratypes (in alcohol): 2 complete specimens (AM W 20718), 1 complete specimen (LACM-AHF 1536), 1 complete specimen (USNM 142107). Paratypes (embedded in Spurr's resin), same locality, June 1987, coll. G. Rouse: 1 block with 2 incomplete specimens (AM W 20719), 2 blocks each with 2 incomplete specimens (LACM-AHF 1537, 1538), 1 incomplete specimen (USNM 142108). Paratype (embedded in Spurr's resin), same locality, collected late 1988, coll. G. Rouse: 1 block with 2 incomplete specimens (AM W 20720).

Description.—Holotype complete with 8 thoracic and 3 abdominal setigers. Total body length 2.0 mm; branchial crown comprising 0.5 mm of this length; maximum width about 0.3 mm. Body cylindrical, short; widest at midthorax with slight tapering anteriorly and posteriorly (Fig. 3A). Distal ends of radioles filamentous, about same width as pinnules. Five to 7 pairs of pinnules per radiole; all terminating at about same height as radioles. Dorsalmost pair of radioles of

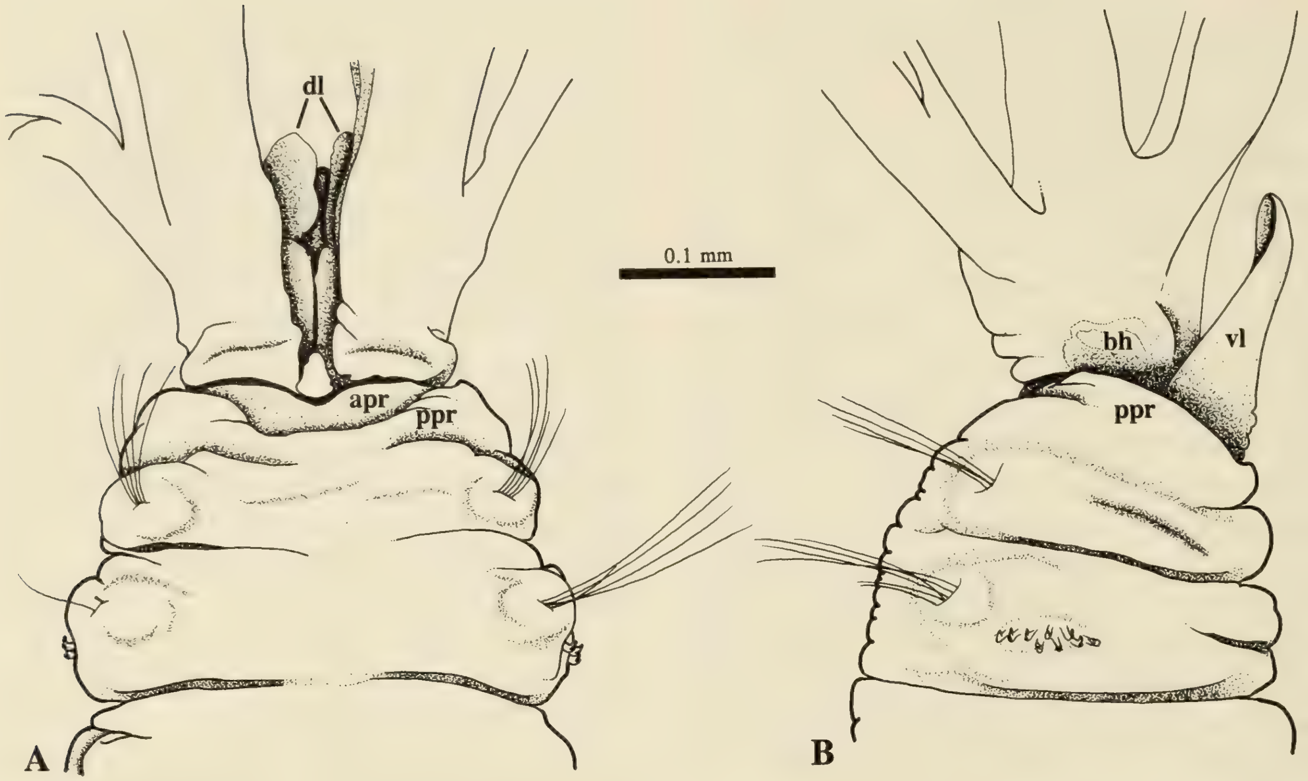

Fig. 1. *Parafabricia ventricingulata* (Paratype, AM W 20718). A, B, Dorsal and lateral (right side) views of anterior end, respectively. Abbreviations: apr—anterior peristomial ring; bh—branchial heart; dl—dorsal lips; ppr—posterior peristomial ring; vl—ventral lobe extension of anterior peristomial ring.

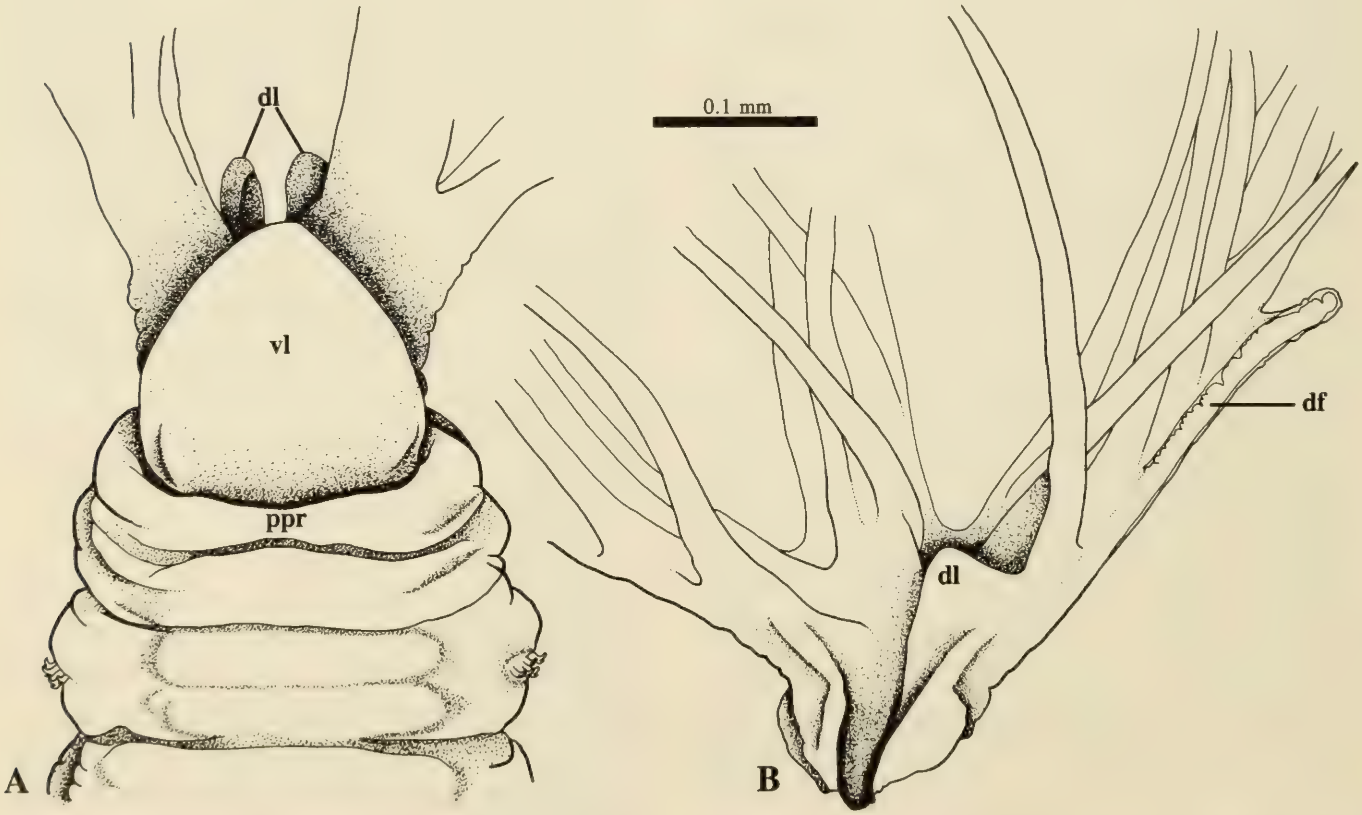

Fig. 2. *Parafabricia ventricingulata* (Paratypes, AM W 20718). A, Anterior end, ventral view; B, Right half of branchial crown, inner view. Abbreviations: df—filamentous appendage on dorsalmost radiole; dl—dorsal lips; ppr—posterior peristomial ring; vl—ventral lobe extension of anterior peristomial ring.

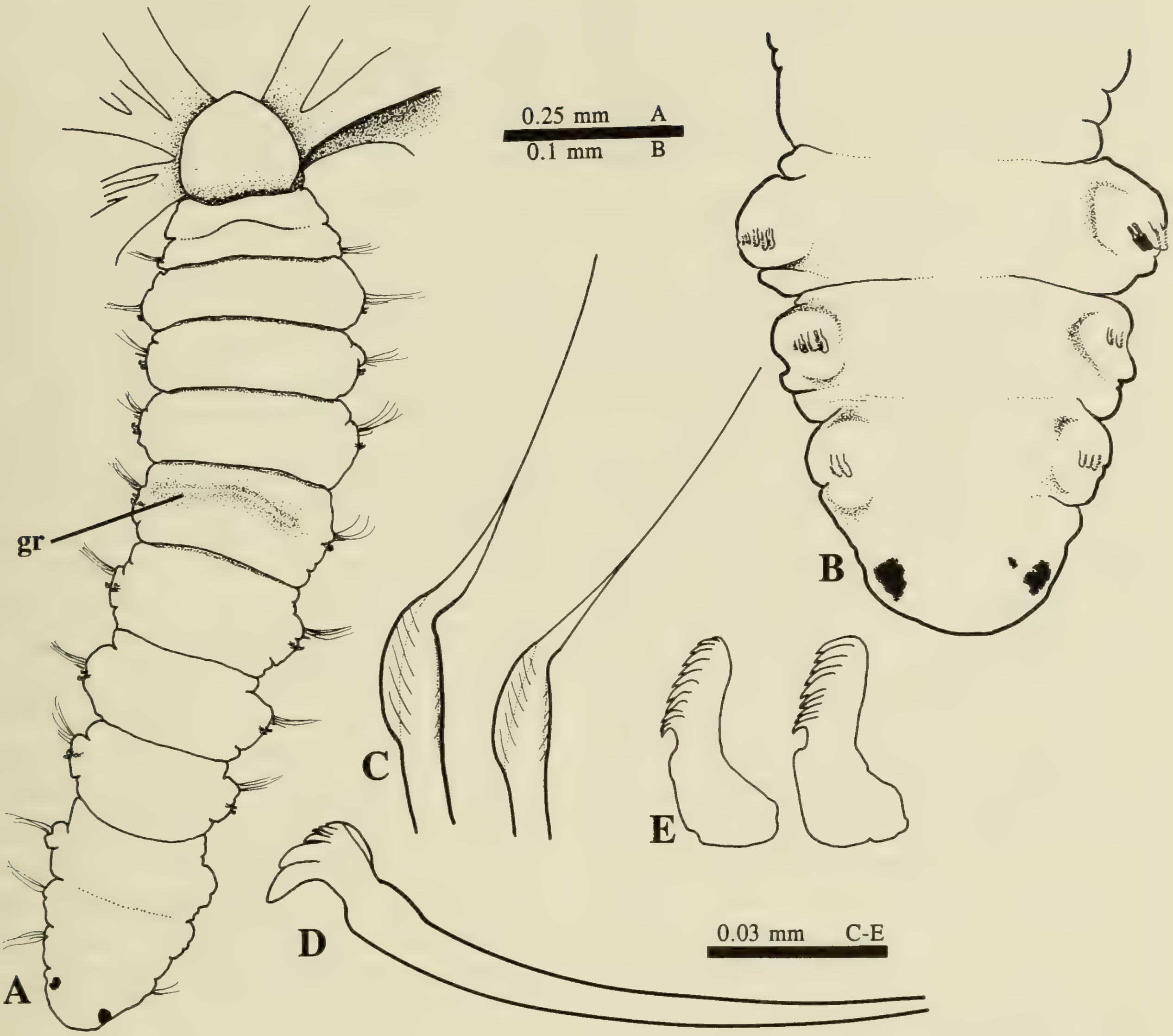

Fig. 3. *Parafabricia ventricingulata* (Paratypes, AM W 20718). A, Ventral view of thoracic and abdominal regions; B, Posterior end, dorsal view; C, Thoracic notosetal pseudospatulate setae from setiger 4; D, Thoracic uncinus from setiger 5; E, Abdominal uncini from setiger 9. Abbreviations: gr—"glandular" ridge on setiger 5.

large animals (>2.0 mm total length) each with an unbranched, vascularized filament extending from radiole margin closest to dorsal midline of body (Fig. 2B); free end of filaments short, distally blunt, about same width as radioles; large blood vessel in filament continues proximally into radiole, giving appearance of filament being fused to radiole margin for most of length. Dorsal lips erect, triangular, distally rounded (Figs. 1A, 2). Anterior margin of anterior peristomial ring only visible middorsally as low shelf (Fig. 1A); ventrally as broad, thin lobe, widest proximally, broadly rounded distally, about 2.0–2.5 times longer than posterior peristomial ring (Figs. 1B, 2A, 3A). Posterior peristomial ring with slightly inflated appearance dorsolaterally, laterally, and ventrally, extending over and covering anterior ring dorsolaterally and laterally, lowest middorsally to form wide gap (Fig. 1A). Annulation between anterior and posterior peristomial rings only visible middorsally and ventrally. Pair of peristomial eyes in anterior or posterior peristomial ring, round, deeply set within body and indistinct. Pygidial eyes round, usually with irregular borders, black (Fig. 3A, B). Low, transverse "glandular" ridge on ventral anterior half of setiger 5 (Fig. 3A), very distinct in animals with surrounding pigmentation, ridge unpigmented, white to cream colored. Anterior peristomial ring (exclusive of ventral lobe) about same length as posterior ring. Setiger 1 about same length as, or slightly longer than, posterior peristomial ring (Fig. 3A); setigers 2–4 each about same length as setiger 1 or each successively longer; setigers 5–8 each about same length as setiger 4 or slightly longer. Setiger 9 about same length as setiger 8, setigers 9–10 each successively shorter. Pygidium about same length as setiger 11, very broadly rounded posteriorly (Fig. 3A, B). Superior thoracic notosetae elongate, narrowly hooded; 4–5 per fascicle. Inferior thoracic notosetae of setigers 2 and 8 short, elongate, narrowly hooded; 2–3 per fascicle; setigers 3–7 each with 2 pseudospatulate setae with very long, drawn out tips (Fig. 3C). Abdominal neurosetae modified, elongate, narrowly hooded; 3–5 per fascicle. Five to 9 thoracic acicular uncini per fascicle (Fig. 3D), forming two slightly staggered rows. Abdominal uncini as rasp-shaped plates (Fig. 3E); 10–11 rows of teeth in profile, 4–6 teeth per row; manubrium about same length as dentate region, constricted distally and slightly expanded proximally; 12–17 uncini per fascicle. Large individuals usually with dark brown pigmentation on branchial lobes just dorsal to dorsal lips, proximal regions of radioles light brown; crown of small individuals usually cream colored or only lightly pigmented. Anterior and posterior peristomial rings and anterior thoracic setigers light to dark brown, fading in posterior setigers with abdomen and pygidium cream colored. Tubes fragile, composed of fine white coral sediment and mucus (G. Rouse, pers. comm.).

Etymology.—The specific epithet refers to the ventral "glandular" ridge on setiger 5.

Remarks.—The "glandular" ridge in *P. ventricingulata* is most prominent in specimens with pigmentation extending back through this region since the ridge itself is not pigmented. Because pigmentation is not as extensive in smaller individuals, the ridge is usually not visible, and in larger specimens lacking pigment in setiger 5, the ridge is very indistinct even with methyl green staining since the ridge does not take up stain and the surrounding area only stains lightly. In some stained specimens, ventral intrasegmental grooves in anterior thoracic setigers (e.g., Fig. 2A) will not stain, thus mimicking the condition seen in setiger 5.

Based on available material, the odd filamentous structures extending from the dorsalmost radioles (Fig. 2B) do not develop until the specimens reach a minimum total length of about 2.0 mm. Intermediate growth conditions of this filament are absent in smaller individuals and there is no evidence of the structure within the radiole. A similar structure is described by Fitzhugh (1990a:10, fig. 6A) from the second pair of radioles of *Novafabricia chilensis* (Hartmann-Schröder). In this latter instance, however, Fitzhugh interpreted this filament as a proximalmost pinnule. The filaments in *P. ventricingulata* do not appear to be pinnules since all pinnules form paired groups and the former structure arises after the proximal pinnules have formed.

Systematic Relationships of *Monroika* and *Parafabricia* to other Fabriciinae Taxa

Figs. 4–8; Tables 1, 2

The positions of *Monroika* and *Parafabricia* within the Fabriciinae were determined from a cladistic analysis involving 36 species and 21 characters. Outgroup considerations follow from the analyses carried out by Fitzhugh (1991a).

New characters and states.—Twenty-one characters, totaling 40 apomorphic states, were used in the present analysis (Table 1). Most characters and states used here have been described and applied by Fitzhugh (1989, 1990a, 1990b, 1990c, 1990d, 1990e, 1991a, 1991b). Modifications of one of these characters and the introduction of three new characters are discussed here.

Development of the breast into a ma-

Table 1.—Characters and states used to determine cladistic relationships of *Monroika africana* and *Parafabricia ventricingulata* to other fabriciin taxa. State "0" is plesiomorphic based on outgroup comparisons (see text). Order of multistate characters does not imply any views on transformation series

1. Ventral filamentous appendages: (0) absent; (1) nonvascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
2. Dorsal lips: (0) well-developed, triangular lobe; (1) low narrow ridge; (2) absent.
3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally somewhat; (2) extensively shifted dorsally.
4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate and/or with a peduncle-like process.
5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a narrow lobe; (1) low membranous collar; (2) membranous collar low dorsally and laterally, higher ventrally; (3) very high membranous collar; (4) low ridge dorsally and laterally, ventrally as a broad lobe; (5) low ridge dorsally and laterally, ventrally as a tongue-like lobe; (6) low ridge all around; (7) low ridge all around except for dorsolateral lobes.
6. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and surface smooth.
7. Dorsolateral incisions on anterior margin of anterior peristomial ring collar: (0) absent; (1) present.
8. Anterior peristomial ring dimensions: (0) wider than long; (1) at least as long as wide.
9. Peristomial eyes in lateral view: (0) well developed and round; (1) poorly developed and crescentic; (2) absent.
10. Distribution of inferior thoracic pseudospatulate notosetae, in setigers 2–8: (0) absent; (1) 2–5; (2) 3–5; (3) 3–6; (4) 3–7; (5) 3–8; (6) broadly hooded, flagellate in 3–7.
11. Thoracic uncini: (0) without large tooth above main fang; (1) large tooth above main fang.
12. Thoracic uncini main fang: (0) slender; (1) swollen.
13. Abdominal uncini teeth: (0) >1 row of teeth; (1) 1 row of teeth.
14. Abdominal uncini breast: (0) oriopsis-like; (1) manubrium about 2.0 times longer than dentate region; (2) manubrium about 1.5 times longer than dentate region; (3) manubrium same length as dentate region.
15. Pygidial eyes: (0) absent; (1) present.
16. Radioles: (0) 3 or more pairs; (1) 2 pairs.
17. Body wall spicules: (0) absent; (1) present.
18. Branchial hearts: (0) absent; (1) present.
19. Displaced pinnules (e.g., *Manayunkia, Monroika*): (0) absent; (1) present.
20. Thoracic uncini shape: (0) typical fabriciin shape; (1) *Manayunkia*/Genus A-type.
21. Pinnule arrangement: (0) distinctly pectinate; reduced to two (1) to four (2) pinnules at bases of branchial lobes.

nubrium in abdominal uncini of Fabriciinae (character 14) has usually been separated into two states (e.g., Fitzhugh 1991a, 1991b): the manubrium being longer than the dentate region or about the same length as the dentate region. This character is now interpreted as comprising three apomorphic states: manubrium about two times longer than the dentate region (state 1), manubrium about 1.5 times longer than the dentate region (2), and manubrium about the same length as the dentate region (3).

The pair of displaced pinnules (character 19) originating just dorsal to the first pair of radioles are discussed under the Remarks on *Monroika*; these appendages being a feature also occurring in some species of *Manayunkia* (Fig. 4A, B; see also the "mediodorsal tentacles" in Pettibone 1953:fig. 1D). The most pressing issue at this time is whether or not these displaced pinnules are homologous to the dorsalmost pinnules in species of *Manayunkia* in which the radioles are supposedly reduced and the pinnules arise directly from the branchial lobes [e.g., *M. aestuarina* (Bourne, 1883), *M. polaris* Zenkevitsch, 1935; Fig. 4C] as opposed to the more typical pectinate arrangement of pinnules along the radioles (e.g., *M. speciosa, M. baicalensis*).

For example, in some *Manayunkia* species, such as *M. aestaurina* and *M. polaris*

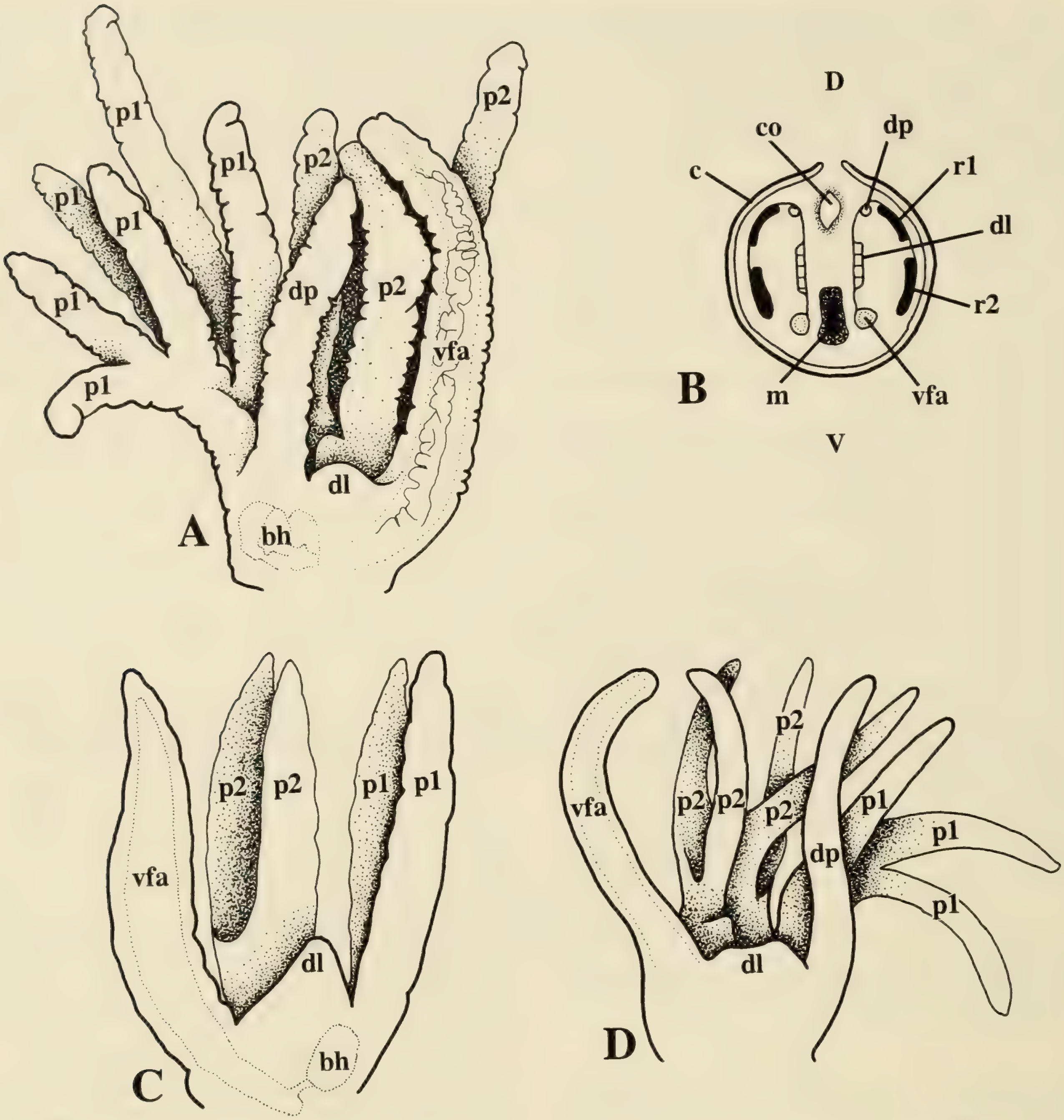

Fig. 4. Branchial crown structures of representative *Manayunkia* species. All radiolar appendages are interpreted as pinnules (see text for explanation). A, Left half (inner margin) of branchial crown of *Manayunkia speciosa* Leidy (LACM-AHF 3432). B, Schematic arrangement (adapted from Banse 1956:fig. 6.2b$_2$) of anterior thoracic and branchial crown structures of *M. speciosa*. C, D, Right half of branchial crown (inner margin) of *M. aestuarina* (Bourne; modified from Banse 1956:fig. 6.1b$_1$) and *M. brasiliensis* (modified from Banse 1956: fig. 4a), respectively. Abbreviations: bh—branchial heart; c—anterior peristomial ring collar; co—cone-like structure; D—dorsal margin; dl—dorsal lip; dp—displaced pinnule; m—mouth; r1—dorsalmost radiole; r2—ventralmost radiole; p1—pinnule of dorsalmost radiole; p2—pinnule of ventralmost radiole; V—ventral margin; vfa—vascularized, ventral filamentous appendage.

(Zenkevitsch 1935:196, fig. 3), the dorsalmost pinnules in each half of the branchial crown (Fig. 4C) arise adjacent to the dorsal lips as seen in displaced pinnules. Displaced pinnules also appear to occur in *M. brasiliensis* Banse, 1956 (Fig. 4D), a species with a branchial crown construction intermediate to that of *M. speciosa* and *M. aestuarina.*

Whereas displaced pinnules clearly occur in some *Manayunkia* species (e.g., Fig. 4A, B, D) and appear to be in *Monroika africana,* a more fundamental problem centers on 1) the relationship of these pinnules to the putative pinnules in species like *M. aestuarina* (Fig. 4C) and *M. polaris,* 2) the presence of paired as opposed to unpaired pinnules, and 3) the presence or absence of distal filamentous radiolar ends.

The most common condition in sabellid radioles is where the distal end of a radiole terminates to a slender filament (e.g., Perkins 1984:fig. 4A; Fitzhugh 1989:figs. 12B, C, 13C). Typically, pinnules are arranged in a paired series along most of the radiole length, with pinnules of a pair lying slightly oblique to one another. Unpaired pinnules can be found in the dorsalmost radiole of each half of the branchial crown of some sabellin species, with one or several of these (unpaired) pinnules enlarged and/or fused to the dorsal lips (Orrhage 1980; = dorsal pinnular appendages sensu Perkins 1984, Fitzhugh 1989).

By extension, if displaced pinnules in *Manayunkia* species are viewed as being unpaired within a radiole, then the dorsalmost radiole of *M. speciosa* in Fig. 4A has one unpaired pinnule (the displaced pinnule) and three groups of paired pinnules but with no distal filamentous end to the radiole. Conversely, if the filamentous radiole end is considered present, there are three pairs of pinnules, with the displaced pinnule a member of the proximalmost pinnule pair. *Manayunkia brasiliensis* (Fig. 4D) then has either one unpaired pinnule and one group of paired pinnules and a long filamentous end to the radiole or else lacks the filamentous radiole end and has two pairs of pinnules. Similar interpretations can be applied to *M. aestuarina,* with the implication that either a single pinnule and filamentous radiole are present or there are only a pair of pinnules (Fig. 4C). In either case, if the strict criterion of position is applied, then the dorsalmost pinnule in *M. aestuarina* is homologous to a displaced pinnule, though the state of being displaced is really not evident. Since such a relationship has yet to be determined, I am taking a conservative approach and assume that species such as *M. aestuarina* and *M. polaris* have reduced radioles, each represented by one pair of pinnules (Fig. 4C) and that the dorsalmost pinnules are not displaced.

The arrangement of pinnules (character 21) can be distinguished as arising in a pectinate pattern (state 0; Fig. 4A) as opposed to the extremely reduced condition (state 1; Fig. 4C) typical of *M. aestuarina* and *M. polaris,* or an intermediate condition (state 2; Fig. 4D) seen in *M. brasiliensis.*

The general shape of the distal ends of thoracic uncini (character 20) within the Fabriciinae can be of two forms. In the plesiomorphic state (0), also seen in plesiomorphic Sabellinae taxa, teeth above the main fang are not very numerous and do not form a dense, crowded group above the main fang (see, e.g., Rouse 1990:figs. 1g, 3f, 4f). In the apomorphic condition (state 1), seen in species of Genus A (Fitzhugh 1989, including *Augeneriella dubia* Hartmann-Schröder, 1965) and *Manayunkia,* teeth above the main fang are very small, numerous and crowded together to give the entire distal ends of uncini a very distinctive profile. This condition is clearly shown in SEM micrographs of *A.* cf. *dubia* by Rouse (1990:fig. 6f, g). Unfortunately, this state has not been accurately illustrated for *A. dubia* (e.g., Hartmann-Schröder 1965:fig. 85) or *Manayunkia* species (e.g., Bourne 1883:plate IX, figs. 10, 11; Zenkevitsch 1925:fig. Ge, 1935: fig. 5d; Annenkova 1928:plate IV, fig. 11; Banse 1956:fig. 4f; Light 1969:fig. 1; Hutchings et al. 1981:fig. 1d).

Taxa included in the analysis.—Thirty-six species from among 10 genera were included in the analysis (Table 2). Most of these species are the same as those used in the analysis performed by Fitzhugh (1991a). Exceptions include the addition of *Monroika africana* and *Parafabricia ventricingulata,* and four species based on work by Fitzhugh (1991b): *Pseudofabriciola capensis*

Table 2.—Character-state matrix for 36 fabriciin species based on character states presented in Table 1.

	Characters and states																				
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Manayunkia speciosa	2	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0
M. baicalensis	2	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0
M. aestuarina	2	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1
M. brasiliensis	2	0	0	0	2	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	2
M. polaris	2	0	0	0	2	0	0	0	0	3	0	0	0	1	0	1	0	1	0	1	1
Monroika africana	2	0	0	0	2	0	0	0	2	2	1	0	0	3	0	1	0	1	1	0	0
Augeneriella dubia	2	0	0	0	4	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0
Genus A	2	0	0	0	4	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0
Fabriciola baltica	1	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
F. berkeleyi	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
F. ghardaqa	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
F. tonerella	1	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
F. mediaseta	1	0	0	0	1	0	0	0	0	6	0	0	0	1	1	0	0	1	0	0	0
Pseudofabriciola australiensis	2	0	0	1	3	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0
P. longa	0	1	0	1	3	2	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0
P. incisura	2	0	0	1	3	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0
P. capensis	0	0	0	1	3	1	1	0	0	0	1	0	0	3	1	0	0	1	0	0	0
P. filamentosa	0	?	0	1	3	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0
P. californica	0	0	0	1	3	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0
Fabricia stellaris	0	0	0	0	4	0	0	0	0	4	1	0	0	1	1	0	0	1	0	0	0
Augeneriella hummelincki	3	0	0	0	4	0	0	0	0	3	1	0	0	1	1	0	0	1	0	0	0
A. lagunari	3	0	0	0	4	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0
A. pectinata	3	0	0	0	4	0	0	0	0	3	1	0	0	3	1	0	0	1	0	0	0
A. basifurcata	3	0	0	0	4	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0
A. mossambica	3	0	0	0	4	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0
Novafabricia chilensis	0	1	0	0	5	0	0	0	0	3	1	0	1	3	1	0	0	1	0	0	0
N. gerdi	0	1	0	0	4	0	0	0	0	2	1	0	1	3	1	0	0	1	0	0	0
N. infratorquata	0	1	0	0	4	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0
N. triangularis	0	1	0	0	4	0	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0
N. tenuiseta	0	1	0	0	4	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0
Parafabricia ventricingulata	0	0	0	0	4	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0
Fabricinuda limnicola	2	2	0	0	6	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
F. bikinii	2	2	2	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
F. trilobata	2	2	1	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
F. pseudocollaris	2	2	0	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0
F. pseudopalpa	0	0	0	0	7	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0

(Monro, 1937), *P. filamentosa* (Day, 1963), *P. californica* Fitzhugh, 1991b, and *Augeneriella mossambica* (Day, 1957). Two additional *Manayunkia* species have been included, *M. baicalensis* and *M. polaris,* in an attempt to account for variability in branchial crown construction (see above) and thoracic inferior pseudospatulate setal distributions. Character states for these latter two species were determined from the original descriptions.

Cladistic methods.—Minimum-length cladograms were constructed from the character state matrix (Table 2) using the commands **mhennig*; bb*** of the program **Hennig86** (Farris 1988). All characters were given equal weight and multistate characters were treated as nonadditive. Character

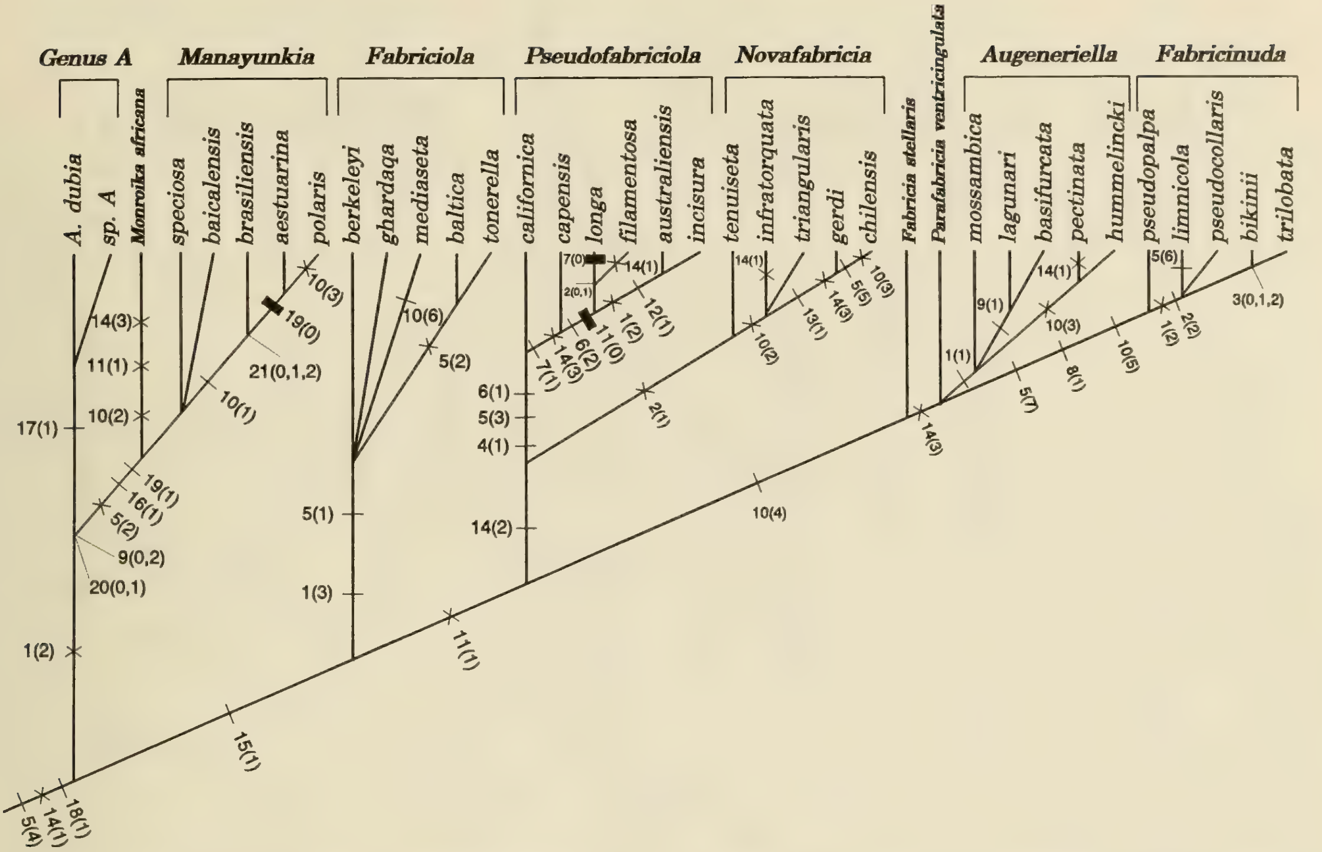

Fig. 5. One of 412 minimum-length cladograms for fabriciin taxa based on character-state distributions (Table 2), in which *Monroika* is a sister group to *Manayunkia.* Length is 60 steps, ci = 0.68, ri = 0.86. See Table 1 for explanations of character-state changes. Slashes on stems denote synapomorphies, X's are homoplasies, and black rectangles indicate reversals; ambiguous character-state assignments are indicated at the nodes.

consistency indices and character state transformation series on cladograms were determined from the **xsteps** command with the **h** and **c** options, respectively.

Results.—A total of 412 minimum-length cladograms were produced from the data matrix (Table 2), each with a length of 60 steps, a consistency index (ci) of 0.68, and a retention index (ri; Farris 1988, 1989) of 0.86.

In most respects, relationships at the generic level are consistent with results obtained by Fitzhugh (1991a, 1991b; e.g., Fig. 5). Topological ambiguity exists at this level with respect to two genera. In one case, *Fabriciola* is either the sister group of *Monroika* and *Manayunkia* (Fig. 6) by the presence of the membranous collar of the anterior peristomial ring [state 5(2)] or is the sister group to the clade containing *Fabricia, Augeneriella, Novafabricia* Fitzhugh, *Pseudofabriciola, Fabricinuda,* and *Parafabricia* (Fig. 5), defined by the presence of pygidial eyes [state 15(1)]. In the other situation, *Monroika* can be the sister taxon to *Manayunkia* (Figs. 5, 6) by the common presence of two pairs of radioles [state 16(1)] and displaced pinnules [state 19(1)], or else situated within *Manayunkia* (Figs. 7, 8) as either a sister group to species with pectinately arranged pinnules [state 21(0)] or a sister group to species with nonpectinate pinnules. The placement of *Monroika* as a sister group to *Manayunkia* is predicated on the ambiguous distribution of states for peristomial eyes (character 9) and shape of thoracic uncini (character 20).

In all cladograms, *Parafabricia* forms a trichotomy with *Augeneriella* and *Fabricinuda* (e.g., Fig. 5), this clade being defined

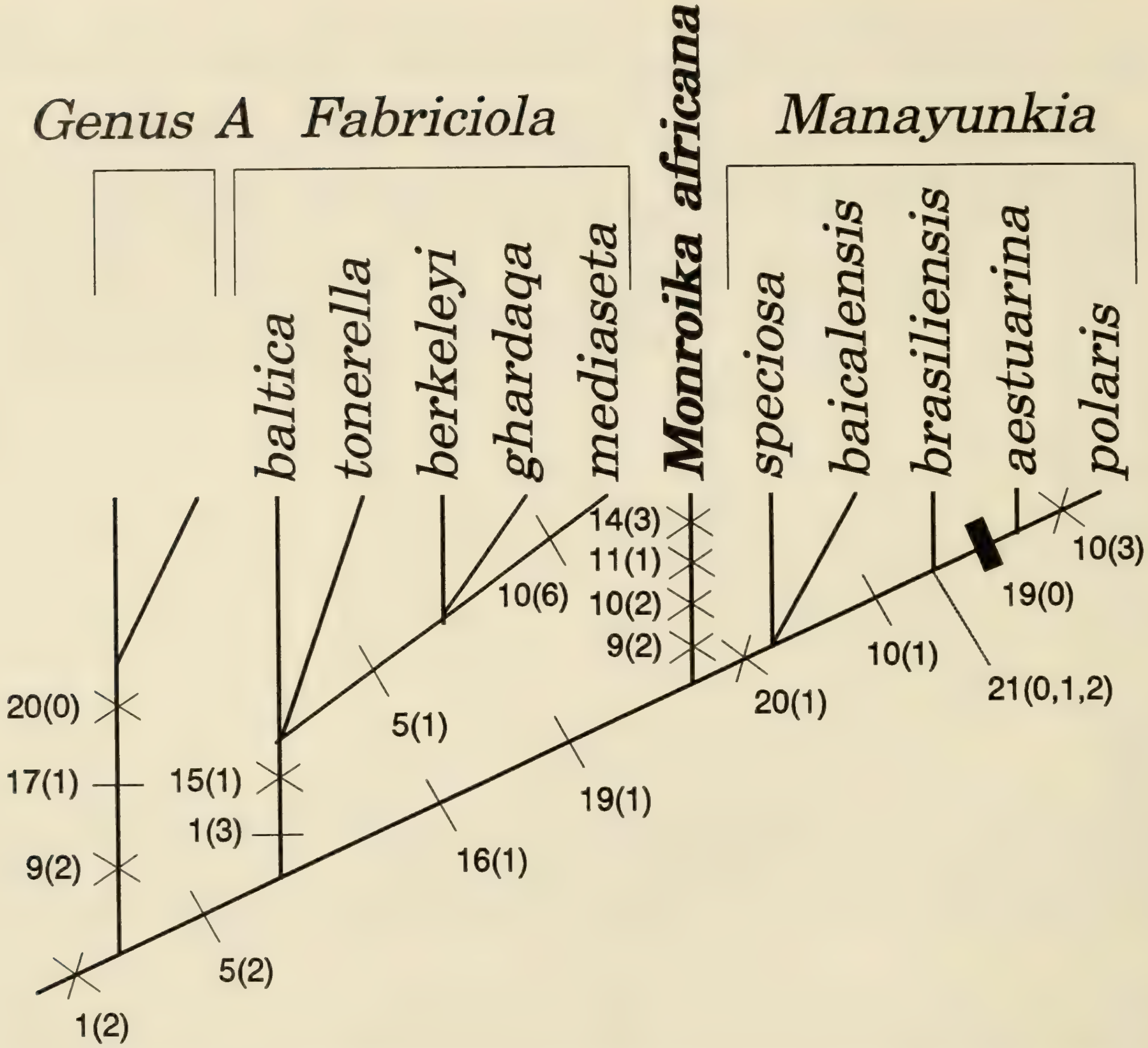

Fig. 6. A portion of a minimum-length cladogram for fabriciin taxa based on character-state distributions (Table 2), in which *Fabriciola* and *Monroika* are sister taxa to *Manayunkia*. Length is 60 steps, ci = 0.68, ri = 0.86. See Table 1 for explanations of character-state changes. All character-state changes are indicated; see Fig. 5 for explanations of symbols.

by the presence of abdominal uncini with a manubrium the same length as the dentate region [state 14(3)]. The sister group to this clade is *Fabricia*, represented here by *F. stellaris* Müller.

The large number of cladograms is primarily due to the numerous possible arrangements of species within *Manayunkia, Fabriciola, Novafabricia, Pseudofabriciola* and *Fabricinuda*. Patterns of ambiguity in the four latter genera are the same as reported by Fitzhugh (1991a, 1991b). Most notable for the present analysis is that there are 13 possible topologies for the placement of *Monroika africana* within *Manayunkia* (Figs. 7, 8).

Discussion.—In light of the present results, two issues must be taken into consideration concerning the status of *Monroika*. First is the reliability of my interpretations of branchial crown characters. One might argue that until specimens in better condition are made available, it would be best to regard most branchial crown characters as unknown. I considered this alternative in an unpublished cladistic analysis in which most branchial crown characters (i.e., characters 1, 2, 16, 19) were coded as unknown

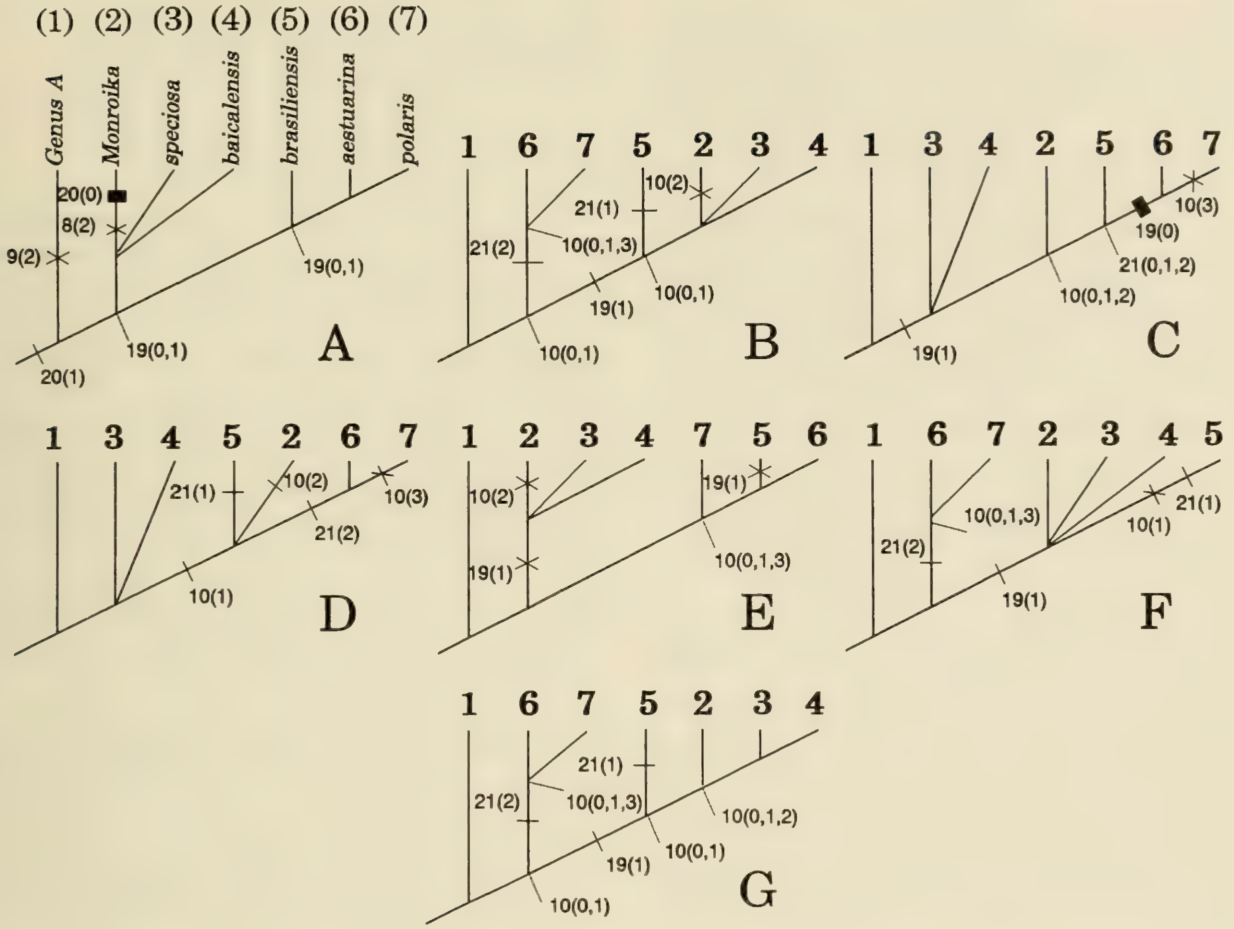

Fig. 7. Seven of 13 possible topologies (see also Fig. 8) among minimum-length cladograms in which *Monroika africana* is placed within the *Manayunkia* clade, based on character-state distributions (Table 2). Relationships among remaining taxa are the same as in Fig. 5. Character-state changes in A are the same as in Fig. 5 except where indicated; changes in B–G are the same as in A except where indicated. See Fig. 5 for explanations of symbols. Taxa in B–G are numbered as in A.

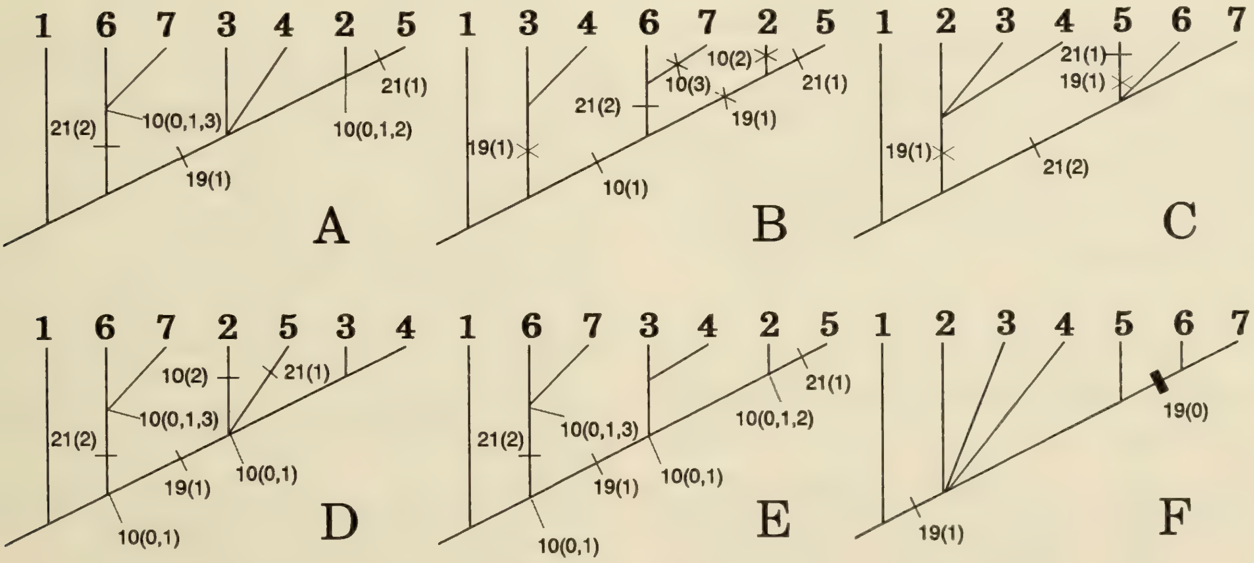

Fig. 8. Six of 13 possible topologies (see also Fig. 7) among minimum-length cladograms in which *Monroika africana* is placed within the *Manayunkia* clade, based on character-state distributions (Table 2). Relationships among remaining taxa are the same as in Fig. 5. Character-state changes are the same as in Fig. 7A except where indicated. Taxa are numbered as in Fig. 7A.

(="?"). All resulting cladograms (totaling over 1200) place *M. africana* out of the clade containing *Manayunkia* and Genus A (cf. Fig. 5) and into the clade containing *Fabricia, Novafabricia, Augeneriella, Fabricinuda,* and *Parafabricia.* Without the influence of these branchial crown characters, this alternative placement is allowed because of the nature of dentition in thoracic uncini (character 11), the distribution of thoracic inferior pseudospatulate setae (character 10), and condition of the manubrium of abdominal uncini (character 14). Since branchial crown characters play such an obvious role in determining the placement of *M. africana,* I am not at this time inclined to suggest placing this species back into *Manayunkia* though present character interpretations fully support such a move.

The second issue is the practicality of maintaining *Monroika* if *M. africana* is in fact a sister species to *Manayunkia* (e.g., Fig. 5). The general arguments for *Monroika* by Hartman (1951) and Jones (1974) are dependent upon the importance of recognizing levels of distinctness and the necessity of acknowledging taxonomic grades. Given the present results, maintaining *Monroika* would neither enhance nor harm the information content of sabellid systematics outside of creating redundancy by maintaining a near identical generic definition and type species diagnosis. If it is subsequently established that *M. africana* is a sister group to or occurs within *Manayunkia,* I would suggest placing this species back into its nominate genus.

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Sincere thanks go to A. I. Muir (BMNH) for the loan of *Monroika africana* specimens, and to L. Ward, Division of Worms, USNM, for carrying this material back to the U.S. and placing it at my disposal. K. Fauchald and L. Ward kindly provided space and equipment during a visit to the Division of Worms. I thank G. Rouse for placing at my disposal the specimens of *Parafabricia ventricingulata.*

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MICROPHTHALMUS SIMPLICICHAETOSUS (ANNELIDA: POLYCHAETA), A NEW HESIONID FROM THE NORTHWESTERN AMERICAN PACIFIC COAST WITH EXCLUSIVELY SIMPLE CHAETAE

Wilfried Westheide and Günter Purschke

Abstract.—The new hesionid species, *Microphthalmus simplicichaetosus,* is described from a sand beach in the Puget Sound, Washington. It differs from the known *Microphthalmus* species in completely lacking compound neurochaetae. The new species is the fourth *Microphthalmus* found on the American northwest Pacific coast.

The hesionid genus *Microphthalmus* Mecznikow, 1865, is distributed worldwide; its species are characteristic faunal elements of tidal and of sublitoral shelly, sandy and sandy-muddy sediments. With one exception, the 27 hitherto known species are typical meiofaunal, mostly interstitial animals revealing a series of morphological and reproductive adaptations to the pore system of sediments (Westheide 1984). Recent unpublished findings suggest that the present number of species is far from complete. Numerous species new to science can be expected. *Microphthalmus simplicichaetosus* is unique within the genus in possessing simple chaetae only. This feature necessitates an emendation of the generic definition as well as of the family diagnosis.

The new species presented here is another result of an ongoing worldwide investigation of meiofauna polychaetes in littoral areas by the senior author. It was found in the course of a sampling tour at the coast of Oregon and Washington in August 1990.

Microphthalmus simplicichaetosus, new species

Fig. 1A–M

Material examined.—About 20 fixed specimens. U.S. Pacific coast: Puget Sound, Henderson Bay, near Wauna (Washington), 47°20′N, 122°38′W, 17 Aug 1990. Low energy beach with poorly sorted sand and gravel, mixed with organic material. Collected from the upper 10 cm layer where the lower beach slope passes into a sheltered sand flat. Extraction of the fauna was carried out with a $MgCl_2$ solution isotonic to seawater. Specimens were fixed with formalin (10%) or Bouin's fluid.

Type material.—Holotype with 26 chaetigers (length 3.1 mm), immature (USNM 136596). Three paratypes in the Zoologisches Museum der Universität Hamburg (Nr. P-20659) and the remaining specimens in the collection of the senior author.

Description.—Length between 0.77 mm (7 chaetigerous segments) and 3.1 mm (26 chaetigerous segments). Width about 140 μm between the segments and 350 μm when parapodia are included. Almost colorless. Prominent prostomium appears almost completely circular from dorsal view. It joins the following segment by a neck-like constriction. There are 5 tentacular prostomial appendages, 2 of them (=paired antennae) dorsally positioned at anterior margin (length about 80 μm), 2 shorter ones (=palps) arising from the ventral side (length about 60 μm), and 1 unpaired tentacle (=antenna) (length about 70 μm) originating from the

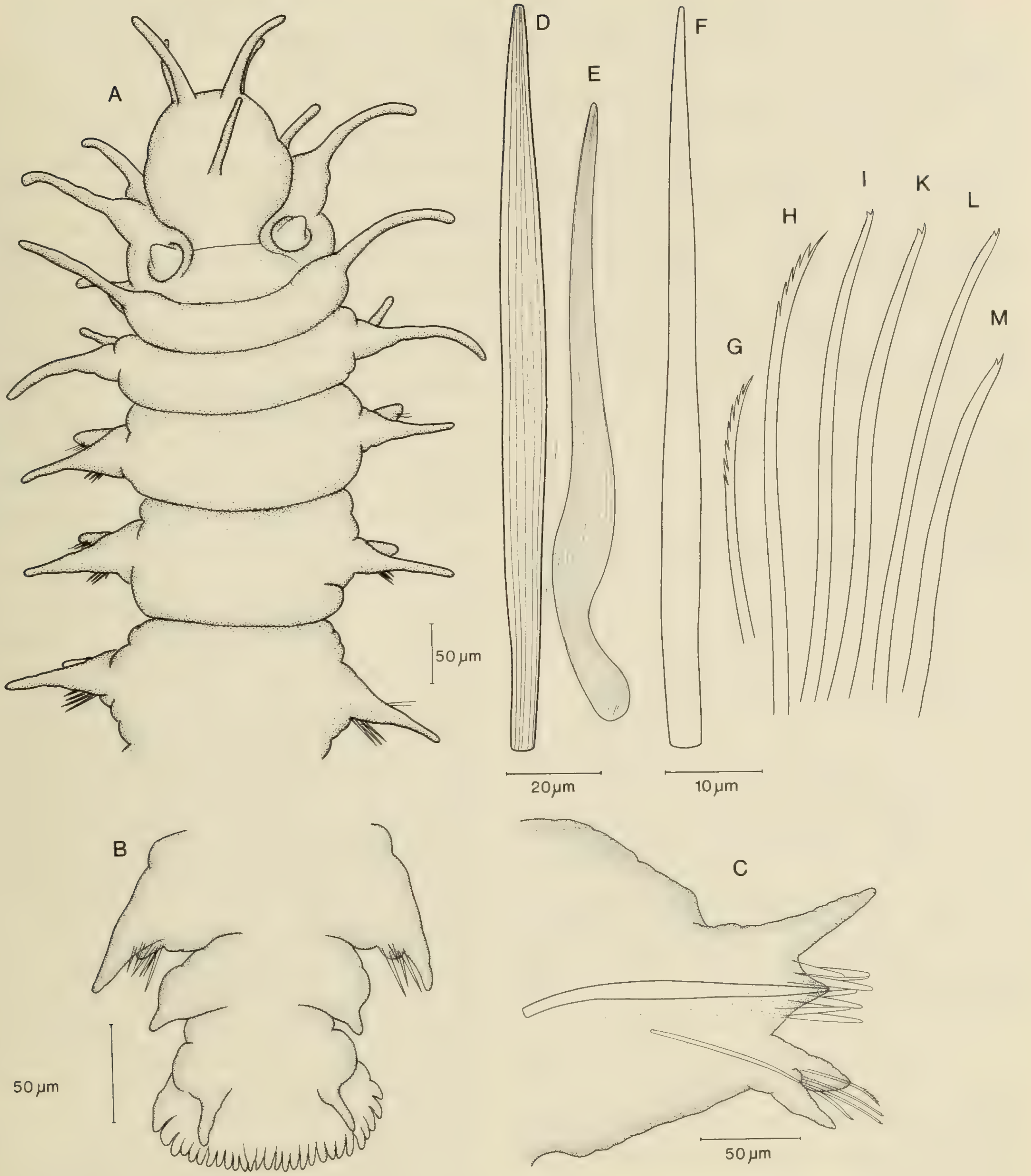

Fig. 1. *Microphthalmus simplicichaetosus,* n. sp. A, Anterior end; B, Posterior end; C, Parapodium from mid-body area; D, Notoacicula; E, Notochaeta; F, Neuroacicula; G, H, Simple serrated neurochaetae; I–M, Simple bifid neurochaetae.

dorsal center (Fig. 1A). Pigmented eyes could not be detected. Two conspicuously protruding nuchal organs situated on first tentacular segment within constriction on both sides behind prostomium.

The 3 following segments are achaetous and each bear 2 pairs of filamentous tentacular cirri. The ventral cirri are considerably shorter than the dorsal cirri. The latter are almost of equal length (about 100 µm), whereas the ventral cirri diminish in length from the first to the third segment (from about 60 to 30 μm). The first ventral pair is partly drawn anteriorly under the prostomium.

The chaetigerous segments are equally shaped and possess almost identical biramous parapodia (Fig. 1C). The notopodial ramus has a relatively short cone-shaped dorsal cirrus as long as or slightly longer than the neuropodial lobe. Below the cirrus there is a bundle of 7 or 8 more or less parallel notochaetae of almost identical shape. They are very stout and slightly tapering with a smoothly rounded apex. Their basal part is slightly bent with a characteristic subproximal constriction and a following distinct dilatation (Fig. 1E). The size of the notochaetae increases markedly from the first to the sixth chaetigerous segment. There is a very stout, somewhat fusiform straight notoacicula with truncated apex (Fig. 1D), which reaches far into the body.

The neuropodial ramus consists of a conical acicular lobe and a broad cone-shaped cirrus directed ventro-posteriorly that does not extend beyond the tip of the lobe. The neuropodium possesses a bundle of up to seven widely protruding chaetae (Fig. 1C), 1 large, straight acicula (Fig. 1F), and possibly also 1 additional very fine acicula. All neurochaetae simple of 2 types: (1) single dorsal serrated chaeta with 5, 6 or 7 distinct subdistal teeth (Fig. 1G, H); (2) up to 6 regularly distally bifid chaetae (Fig. 1J, K, L), the ventral-most of which is shorter and slightly stouter (Fig. 1M). The area below the subdistal tooth of these chaetae is finely structured but could not be resolved by light-microscopy.

One to 3 terminal posterior segments achaetous. Pygidium with a broad anal plate, bearing numerous marginal adhesive papillae and two usually short anal cirri (Fig. 1B).

Anteriorly papillated pharynx a straight tube without any foldings. It projects backwards to the 4th chaetigerous segment. No genital organs or gametes could be observed in the specimens available.

Discussion.—The relatively small body dimensions, number and arrangement of prostomial appendages, the 6 pairs of tentacular cirri, the shape of the parapodia, and the existence of a one-piece papillated adhesive anal plate are typical features of the genus *Microphthalmus* Mecznikow, 1865. The species presented is very close to *M. hartmanae,* which could be shown in a phylogenetic systematic analysis to be the most primitive species within the genus (Westheide 1977). The nominate subspecies *M. hartmanae hartmanae* Westheide, 1977, from Florida and the *M. hartmanae pacificus* Yamanishi, 1984, from Japan and North China (unpublished observations of Zhao Jing and the senior author) possess similar bundles of numerous, stout, uniform notochaetae. Two of the simple neurochaetal types of *M. hartmanae* are also present in the new species: the subdistally serrated ("pectinate") chaeta and the bifid slightly bent chaetae. *Microphthalmus simplicichaetosus,* however, completely lacks heterogomph falcigerous compound chaetae, which are characteristic of all described *Microphthalmus.* Since compound chaetae are characteristic of hesionid taxa, their lack may be considered to be a highly derived (=autapomorphic) feature of the new species. For its inclusion into the diagram of the phylogenetic relationships of the *Microphthalmus* species (see Westheide 1977, fig. 2), two positions are possible. Either the new species is: 1) the sister group of all hitherto known *Microphthalmus* species; or 2) considered to be the sister species of *M. hartmanae.* The very obvious similarity in chaetation between the two species strongly suggests the latter possibility. The diagnosis of the genus *Microphthalmus* thus must be altered as well as that of the family Hesionidae (e.g., see Pettibone 1982) by the following emendation: The neurochaetae are compound falcigers or spinigers, with the terminal blades long to short; there may be some additional simple neurochaetae, "or neurochaetae may be exclusively simple."

The species presented here is the fourth *Microphthalmus* found on the American northwest Pacific coast. The genus was mentioned by Banse & Hobson (1974) and Kozloff (1987) for this area; Fournier (1991) described three species from British Columbia and Washington: *M. hystrix, M. coustalini,* and one that was not named. Together with the specimens of the new species we found another *Microphthalmus* species in the samples from Puget Sound. The single mature specimen is incomplete and lacks the posterior end with anal plate and anal cirri. The chaetation is highly similar to *M. hystrix* Fournier: it comprises the same type of stout distally bent notochaetae, although in a higher number, and identical neurochaetal types. For the time being, the lack of certain details of *M. hystrix* chaetae does not allow its definite identification.

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CLAUSOGNATHIIDAE, A NEW FAMILY OF GNATHOSTOMULIDA FROM BELIZE

Wolfgang Sterrer

Abstract.—*Clausognathia suicauda,* a new genus and species of Gnathostomulida, is described from subtidal sand in the vicinity of Carrie Bow Cay, Belize, and a new family, Clausognathiidae, is created within the lower Bursovaginoidea-Scleroperalia. The novel features of *Clausognathia* consist of the combination of a filospermoid rostrum and sensorium with a scleroperalian pharynx and male system; the relatively anterior position of the male organ; and the differentiation of the hindgut as a solid, lumen-less tissue composed of large, succulent cells. The latter feature might function as a chordoid organ, or be the site of prokaryotic endosymbionts.

Collections of sand-living meiofauna made in the vicinity of Carrie Bow Cay, Belize (Rützler & Macintyre 1982) in 1974, 1984 and 1991 yielded about 20 different species of Gnathostomulida, some of them new. While a complete account of this fauna is now being prepared, the most curious of the new species, which merits erecting a new genus and family, is described herein.

Sediment samples were collected by Scuba, with a bucket, and treated as described previously (Sterrer 1971a). The methods of analyzing and describing specimens and species, including measurements and indices used, are as detailed in Sterrer (1991).

Order Bursovaginoidea Sterrer, 1972

Composition.—Two suborders, Scleroperalia Sterrer, 1972, and Conophoralia Sterrer, 1972.

Suborder Scleroperalia Sterrer, 1972

Composition.—Seven families, Agnathiellidae Sterrer, 1972; Mesognathariidae Sterrer, 1972; Gnathostomariidae Sterrer, 1972; Rastrognathiidae Kristensen & Nørrevang, 1977; Problognathiidae Sterrer & Farris, 1975; Onychognathiidae Sterrer, 1972; and Gnathostomulidae Sterrer, 1972.

Clausognathiidae, new family

Diagnosis.—Scleroperalia with an elongated, pointed rostrum (index greater than 3) that lacks (!) paired sensory organs. Epidermal cells not in stripes. Male stylet of the rod type. Sperm small, round or polygonal. Basal plate may be absent. Jaws lamellar but not closed, without a cauda; teeth uniform, arranged in a ventro-rostral arc. Without a jugum. With the ability to swim backwards.

Clausognathia suicauda, new genus, new species

Figs. 1–3, Table 1

Diagnosis of *Clausognathia* new genus: Clausognathiidae without a basal plate. Posterior portion of gut without a lumen, consisting of highly vacuolized cells. Male organ with a vesicula seminalis and a vesicula granulorum.

Type species: *Clausognathia suicauda,* new species.

Etymology.—Genus from the Latin *clausus* (closed) and the Greek root *gnath-* (jaw), in reference to the usually tightly clenched jaws; species from *sus* (pig) and *cauda* (tail), in reference to the often curled-up tail.

Holotype.—USNM 142377, one specimen in squeeze preparation.

Table 1.—*Clausognathia suicauda,* measurements and statistics.

	$\bar{X}$	*SD*	Max	Min	*n*
Body length of adults	1150.00	70.71	1200	1100	2
Body width of adults	85.00	7.07	90	80	2
Body index of adults	13.54	0.29	13.75	13.33	2
Rostrum index of adults	4.67				1
Jaw length	13.56	1.13	15	12	9
Penis stylet length	28.33	4.51	33	24	3
Sperm length	5.00	0.00	5	5	6
Sperm width	4.67	0.52	5	4	6
Sperm index	1.08	0.13	1.25	1.00	6

Type locality.—Belize (Western Atlantic Ocean), barrier reef south of Carrie Bow Cay. Detritus-rich sand bordered by *Thalassia,* at the shoulder of one of the Southern Sand Bores (reef islets) at 9 m depth; sample collected 18 Apr 1991; 8 specimens.

Other localities.—Belize, barrier reef off Carrie Bow Cay. Fine sand with detritus from the sand trough at 33 m depth; sample collected 19 Apr 1991; 1 specimen.

Diagnosis of *C. suicauda,* new species: Fairly slender *Clausognathia* (body index 13.54) with slender rostrum (index 4.67) and a well defined, fragile tail. Jaws 13.56 μm long, with 10.86 teeth. Sperm round, 5 μm in diameter. Penis stylet 28.33 μm long.

Description.—Organization and behavior: Colorless-translucent to faintly yellowish. The only complete adult (Fig. 2A) was 1100 μm long and 80 μm wide at U 59.1; another adult, which had lost its tail section, was estimated to have had a total length of 1200 μm, and was 90 μm wide at U 53.3. The mean body index of adults is 13.54. The rostrum (Fig. 2B, C) is slender and pointed, 125–140 μm long and 30–35 μm wide (index 4.67). The posterior part of the body usually looks swollen and succulent (Fig. 1), and rather abruptly narrows to an extremely fragile, wrinkled, contractible and usually curled-up tail region of 50–150 μm length. In the petri dish the animal usually appears as a short spiral which turns slowly, reversing direction when the rostrum hits an obstacle. The tip of the rostrum is very flexible and constantly probes its surroundings. Extremely fragile and slow-moving, the animal can easily be mistaken for catenulid turbellarians of the family Retronectidae (Sterrer & Rieger 1974), which are found in the same sample.

The skin is made up of polygonal cells of 5 μm diameter that do not seem to be arranged in any pattern, each carrying a single cilium of 20 μm length. Cilia around the mouth may reach a length of 42 μm (Fig. 2C). There are round epidermal inclusions throughout the body. The sensorium consists of a row of occipitalia (Fig. 2C), single stiff cilia arranged along the dorsal median of the rostrum; some of these are kinked and may reach 35 μm in length. No other sensory cilia, bristles or pits were found, although there is a possibility that single paired cilia (as which the apicalia typically appear) might have been overlooked.

Digestive tract: The oval mouth opening, situated between U 14.1 and U 15.1, is 5–10 μm long and leads into a buccal cavity (Fig. 2B, C) whose epithelium is thickened rostrally (to 20 μm) but seems otherwise devoid of specialized glands. There is no basal plate. The jaws (Figs. 2D–G, 3A–F) are 12–15 μm (mean 13.56 μm) long, delicate, and rather complex under a deceptively simple dorsal outline (Fig. 2D). Being higher than wide, the jaws usually come to lie on the side during squeeze preparation, which makes it difficult to obtain an accurate dorsal view. The jaws are forceps-

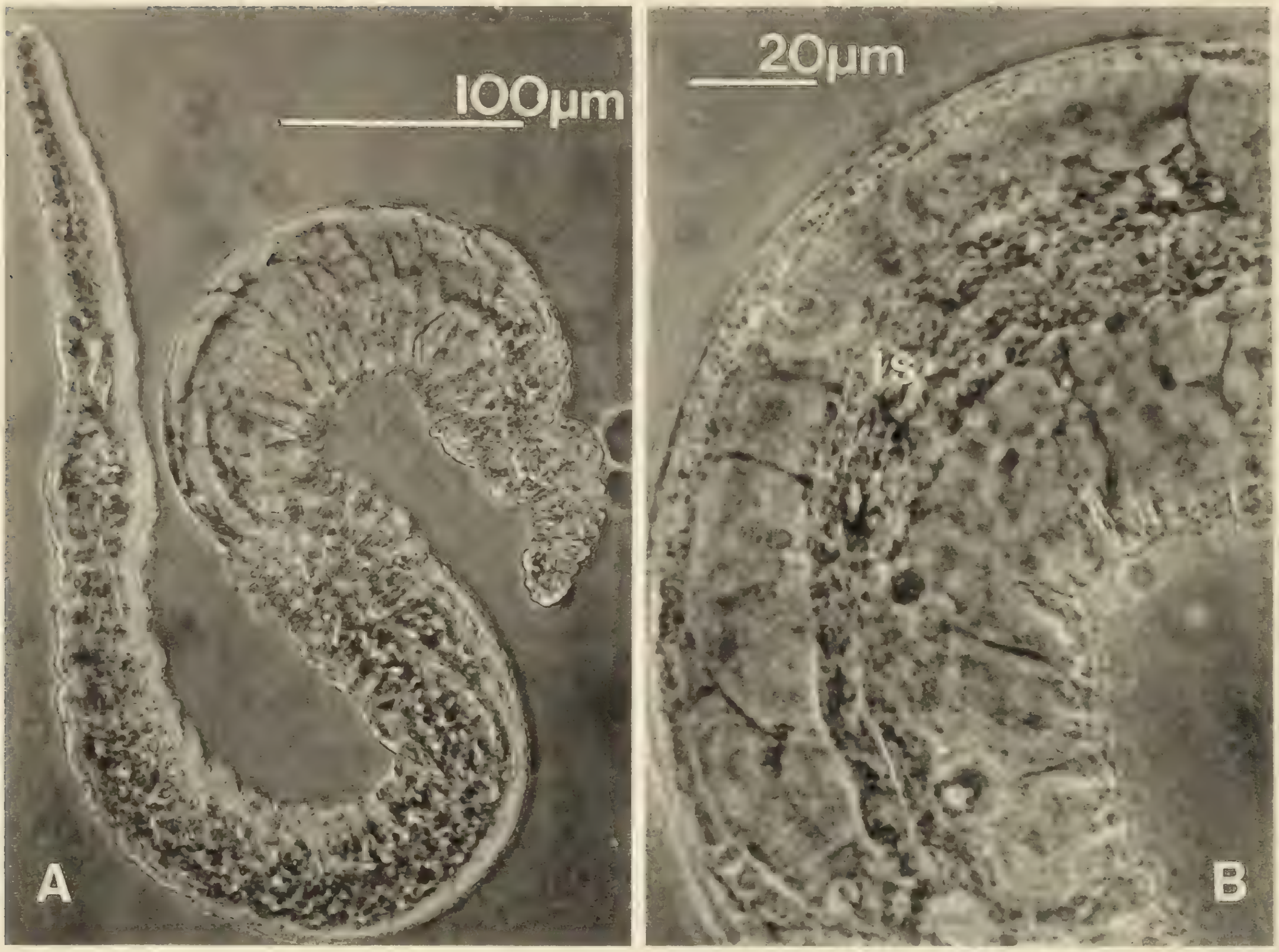

Fig. 1. *Clausognathia suicauda.* A, Habitus of a juvenile; B, Posterior body section of the same individual showing vacuolized cells and "lateral system" (ls). Phase contrast photographs of live specimens.

shaped, with 9–12 (mean 10.86) short but pointed teeth arranged in a dorso-rostro-ventral arc. A crista (cr) flares out dorsolaterally, and a sharp rostral apophysis (ra) points caudo-ventrally. There are "stiffening rods" running from the anterior, tooth-bearing part to the posterior part of the jaws. The symphysis, however, is not reinforced or broadened, and there is no cauda. The posterior third of the jaws is embedded in a muscular pharynx which extends 10–16 μm (mean 12.83 μm) behind the symphysis. The pharynx is neither tripartite, nor does it contain discrete glands. The gut cells, 5 μm high, enclose a well defined lumen (gl) that extends to about U 59. Between U 59 and U 88, i.e., somewhat rostrally of the tail, the body is filled with large, succulent cells that do not seem to enclose a lumen (Figs. 1, 2A, K, L). These cells are flanked laterally by a pair of stringy tissue strands ("lateral system," ls) that originate in the anterior body half, but become prominent only in the region of the succulent cells. Upon squeezing, one specimen produced elongated cells with an equally elongated, dark inclusion (nucleus?) from the neck region (Fig. 2H); although their function is unknown they are reproduced here because of their similarity, in shape and location, with the sperm of some Turbellaria-Retronectidae (Sterrer & Rieger 1974, figs. 10, 13, 14).

Male system: Three specimens had mature male organs (Figs. 2A, I–L, 3G, H), of which the most conspicuous structure is the penis stylet. Situated ventrally, approximately between U 60 and U 63, the stylet is straight, slightly conical, 24–33 μm (mean 28.33 μm) long and 4–5 μm (mean 4.33 μm)

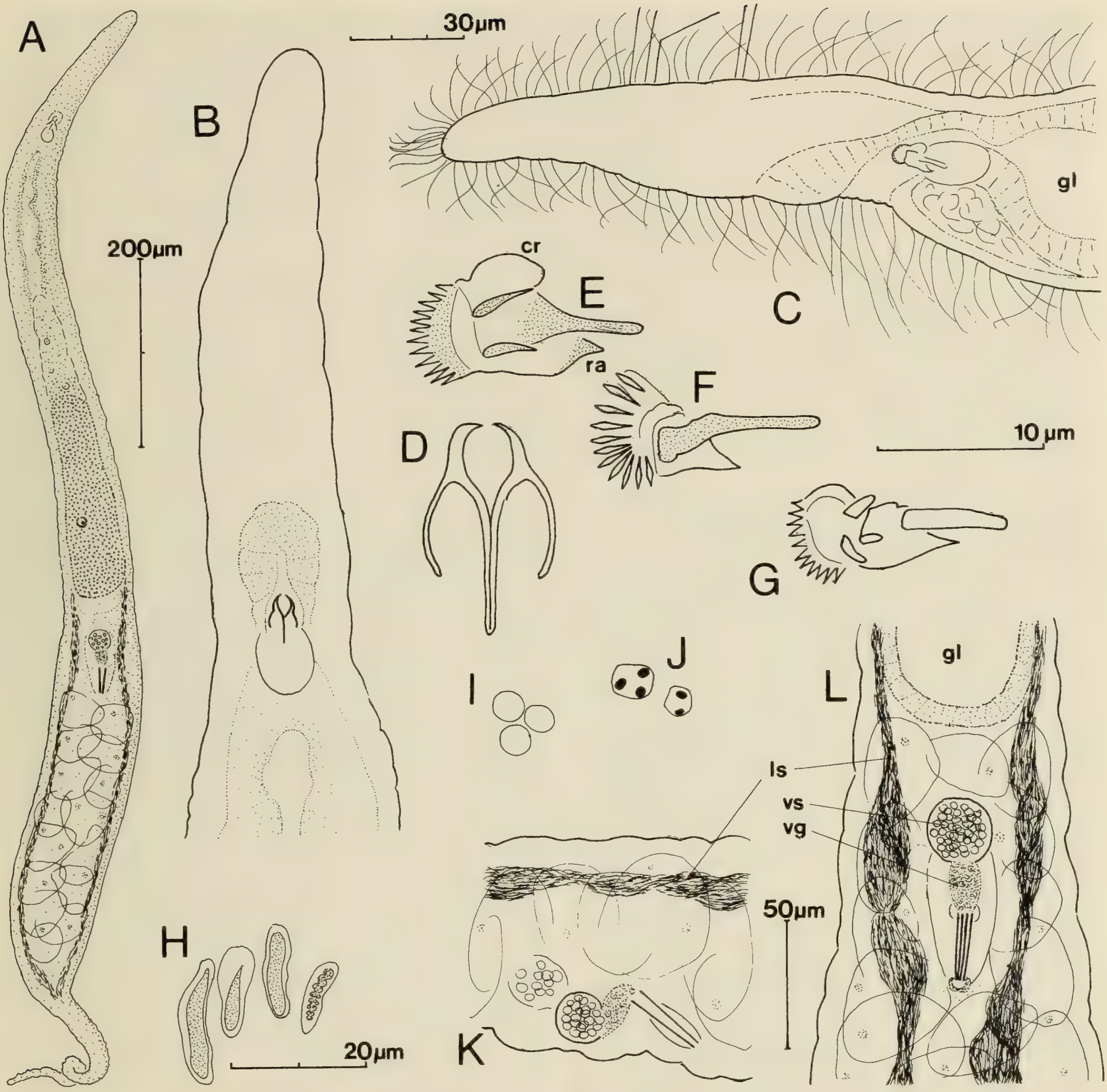

Fig. 2. *Clausognathia suicauda.* A, Habitus of an adult; B, Rostrum and pharyngeal region, dorsal view; C, Rostrum and pharyngeal region, left lateral view; D, Jaws, dorsal view; E–G, Jaws of 3 specimens, left lateral view, showing crista (cr) and rostral apophysis (ra); H, Elongated cells squeezed from neck region; I, Sperm from the vesicula seminalis, in situ; J, The same, squeezed out of the vesicula; K, Male copulatory organ, left lateral view; L, The same in dorsal view, showing gut lumen (gl), "lateral system" (ls), vesicula granulorum (vg), vesicula seminalis (vs) and stylet. Cilia have been omitted except in 2C. Scales apply to A, B–C, D–G, H–J and K–L, respectively.

wide proximally. It consists of 6–8 rods, and the distal two-thirds of its length are surrounded by a fine-grained glandular sheath. Anterior to the stylet there is an ellipsoidal vesicula granulorum (vg), about 20 µm long and 10 µm in diameter, filled with delicate granular secretion in round clusters of 5 µm diameter. Further anterior is the spherical vesicula seminalis (vs; diameter 25 µm), which is filled with sperm. Testes could not be identified with certainty; in one of the specimens the vesicula seminalis appeared to open frontally into an unpaired testis. A male pore is located ventrally of the tip of

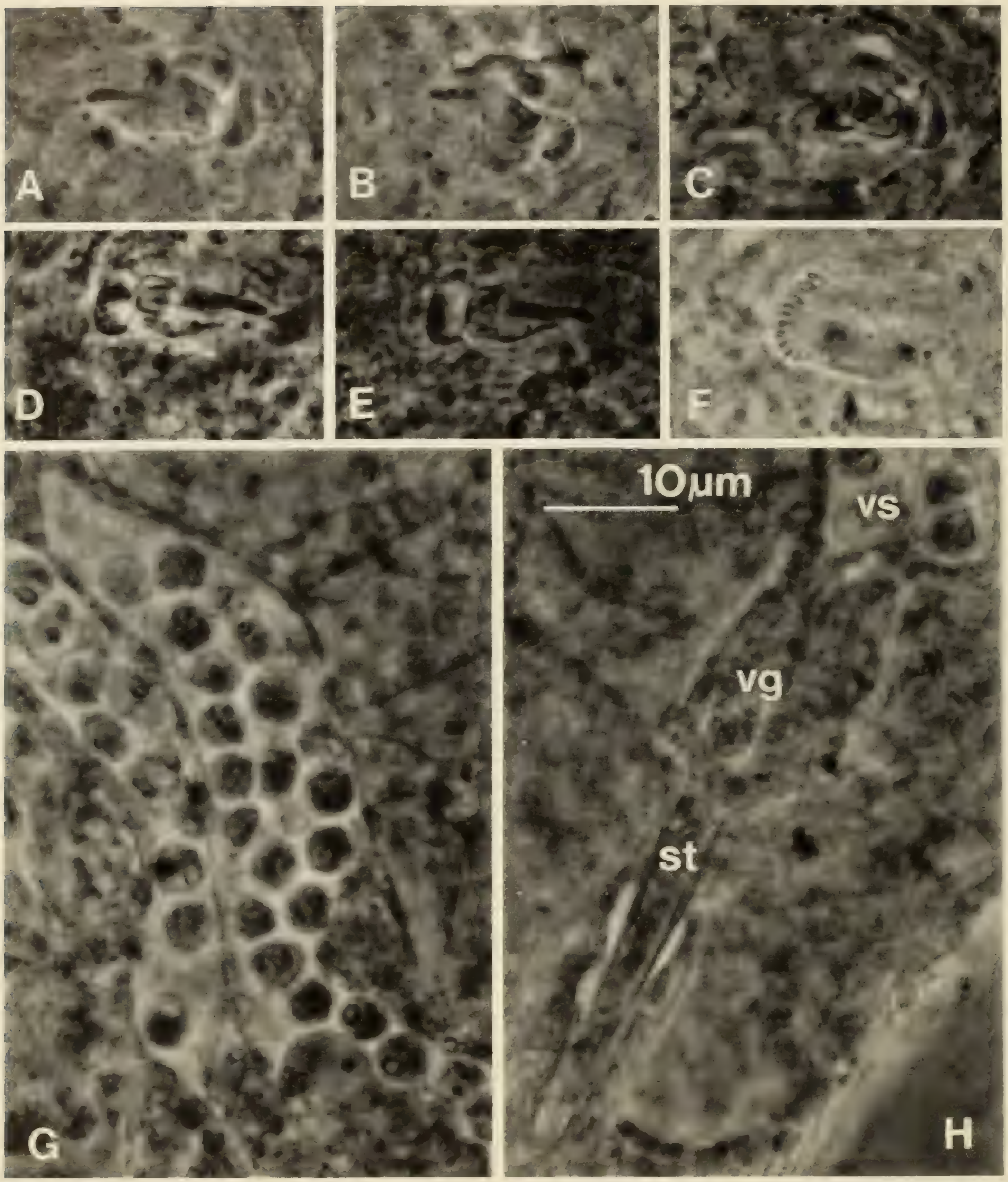

Fig. 3. *Clausognathia suicauda.* A, Jaws, unsqueezed, in right lateral view; B, The same jaws, squeezed; C, Jaws of another specimen, squeezed, in right lateral view; D–F, Jaws of 3 other specimens, unsqueezed, in left lateral view; G, Vesicula seminalis with sperm, squeezed; H, Penis stylet (st), vesicula granulorum (vg) and part of vesicula seminalis (vs), squeezed. Phase contrast photographs of live specimens, all in the same scale.

the stylet (Fig. 2L). One specimen seemed to have a sphincter muscle between the vesicula granulorum and the stylet. The sperm (Figs. 2I, 3G) are globular, 5 µm in diameter, and devoid of any flagellar structure recognizable in the light microscope. Each sperm usually carries 2 or 3 round inclusions that are highly refractile in phase contrast (Fig. 2J).

Female system: The ovary (Fig. 2A), as

seen in two specimens, is dorsal and unpaired, extending between U 27 and U 53; eggs mature caudally, and the largest egg may reach a length of 250 μm. None of the specimens examined had a vagina or bursa, and there was no evidence of sperm outside the male organ.

Discussion.—*Clausognathia* is of particular interest since it combines characters that had hitherto been neatly separated between the two orders of Gnathostomulida (Sterrer 1972). The long, slender rostrum, and the simple sensorium (consisting of nothing but a row of occipitalia) are indistinguishable from those of Filospermoidea; on the other hand, the possession of a penis stylet of the rod type and round sperm of the dwarf type clearly place *Clausognathia* in the Bursovaginoidea, suborder Scleroperalia. Several further characters deserve more detailed attention.

The absence of a basal plate is shared with the genera *Agnathiella* Sterrer, 1971b, *Tenuignathia* Sterrer, 1976, *Rastrognathia* Kristensen & Nørrevang, 1977, and at least two undescribed genera. The jaws are most similar to those of Mesognathariidae, in particular the genus *Mesognatharia* Sterrer, 1966, with regard to the small size, uniformity (absence of a prominent terminal tooth) and arc-like arrangement of the teeth. In dorsal view, the unsqueezed jaws are remarkably similar in outline to those of *Gnathostomaria lutheri* Ax, 1956. General features of the pharynx, such as the absence of discrete glands and the non-tripartite appearance of the pharyngeal bulb, are also shared with lower Scleroperalia.

The differentiation of the hindgut as a solid tissue made up of large, highly vacuolized cells is clearly new among Gnathostomulida. It is most likely derived from a condition found in *Tenuignathia rikerae* (cf. Sterrer 1976, figs. 26, 39) and confirmed in *T. vitiensis* (Sterrer 1991, fig. 10D), where such cells only occupy the dorsal portion of the gut, albeit throughout its entire length. With *Tenuignathia, Clausognathia* shares also a pair of conspicuous tissue strands of unknown function ("lateral system"). Vacuolized tissues and chordoid organs occur in a number of vermiform interstitial taxa (Ax 1966, Schoepfer-Sterrer 1969), and have been functionally interpreted as a turgor skeleton facilitating the locomotion between sand grains. In the case of *Clausognathia,* however, the extreme fragility of the body and weak musculature in general do not support such an interpretation. Another possibility is that the hindgut contains prokaryotic endosymbionts such as described from a number of meiofauna taxa lacking mouth and gut lumen (Ott et al. 1982). This explanation is particularly attractive since Gnathostomulida, which are typically found in anoxic or microxic environments, and often in the company of mouthless Turbellaria-Retronectidae (Sterrer & Rieger 1974), have yet to be shown to contain such endosymbionts.

The male system of *Clausognathia* conforms, in principle, with that of lower Scleroperalia. A vesicula seminalis is present in *Gnathostomaria, Rastrognathia, Mesognatharia* and *Labidognathia.* However, *Clausognathia* stands alone in having a distinct vesicula granulorum. The sperm agrees best in shape and size with that of *Rastrognathia* (Kristensen & Nørrevang 1977, fig. 15) although microvilli were not seen. The absence of a bursa in otherwise mature specimens, finally, has been observed in *Agnathiella beckeri* Sterrer (1971b:222), where one of three adults lacked a bursa, and shown by Riedl (1971) to be a temporary condition in the cycle of bursa replacement. Riedl (1970:229) reports for *Labidognathia* that "a few individuals, characterized by a swollen gut, . . . were of a medium or larger size range and showed no stylet, no bursa, or both were lacking." The observation, in *Clausognathia,* of an incomplete reproductive system (no bursa, no testes) in the presence of a swollen hind gut suggests a cycle in which a feeding phase (such as increased symbiont activity?) alternates with a reproductive phase. However, should the lack of a bursa and/or the possession of only one unpaired testis turn out to be true characters of *Clausognathia,* a new suborder might be called for to accommodate this unique genus.

In view of its overall affinities, the new family Clausognathiidae seems best positioned among the lower Bursovaginoidea-Scleroperalia, in the vicinity of Mesognathariidae, Rastrognathiidae, Agnathiellidae and Gnathostomariidae.

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A NEW PHYLOGENETIC CLASSIFICATION OF THE GENERA OF THE PROTERODIPLOSTOMIDAE DUBOIS, 1936 (DIGENEA: STRIGEIFORMES)

Daniel R. Brooks, Joao Batisto Catto, and Jose F. R. Amato

Abstract.—A new phylogenetic hypothesis, annotated classification, and cladistic diagnoses for the genera of the Proterodiplostomidae (Strigeiformes) are presented, based on information gathered from new collections of proterodiplostomids in *Caiman crocodilus yacare* from Brazil, re-examination of the diversity of terminal genitalia, and polarization of characters based on the outgroups provided by higher level phylogenetic analyses of the strigeiforms. The new phylogenetic hypothesis provides a more efficient summary of character information and increases the degree of support for long-term phylogenetic association between crocodilians and proterodiplostomes.

Members of the Proterodiplostomidae Dubois, 1936 inhabit crocodilian, and occasionally chelonian and ophidian, hosts throughout the range of living crocodilians. The first phylogenetic systematic analysis of the family (Brooks 1979) was performed prior to the formulation of an explicit phylogenetic hypothesis for the higher-level relationships among strigeiform digeneans (Brooks et al. 1985; 1989; Shoop 1989), and suffered from a lack of explicit outgroups. In addition, examination of specimens collected from *Caiman crocodilus yacare* in southwestern Brazil by JBC has led to a new interpretation of the diversity in the genital ducts and terminal genitalia. This report updates and upgrades the phylogenetic systematic hypothesis for the genera of proterodiplostomes.

Materials and Methods

This study is based on examination of specimens of whole mounts and sectioned material for members of all genera of proterodiplostomes, including new material of *Cystodiplostomum, Prolecithodiplostomum, Proterodiplostomum, Paradiplostomum,* and *Herpetodiplostomum* collected in *Caiman crocodilus yacare* from the Pantanal region of southwestern Brazil by JBC. Characters used by Brooks (1979; see also Brooks & O'Grady 1989) were polarized using the phylogenetic relationships among the strigeiforms (Brooks et al. 1985; 1989; Shoop 1989) to determine explicit outgroups. The plesiomorphic state for other conditions of the paraprostate gland was determined by functional outgroup analysis. In addition, the structure and arrangement of the terminal reproductive ducts was re-analyzed as follows.

Among strigeiform digeneans, the plesiomorphic condition for the terminal genitalia is one in which the uterus and cirrus open separately (Shoop 1989). The proterodiplostomes exhibit a unique organ, the *paraprostate gland,* which may join the male duct, join the uterus, or open separately. The male duct and uterine duct may open separately or be fused to form a hermaphroditic duct. The following four conditions occur among proterodiplostomes:

(1) Paraprostate and male ejaculatory duct fused, uterus separate (*Ophiodiplostomum, Heterodiplostomum, Petalodiplostomum, Neelydiplostomum,* and *Pseudoneodiplostomum*).

(2) Paraprostate and male ejaculatory duct fused, and uterus fused to that common duct forming a hermaphroditic duct (*Pseudocrocodilicola, Polycotyle,* and *Crocodilicola*).

(3) Paraprostate fused with uterine duct, and those fused with ejaculatory duct to form a hermaphroditic duct (*Archaeodiplostomum*).

(4) Paraprostate not fused with male duct, opening separately into genital atrium (*Mesodiplostomum, Cystodiplostomum, Prolecithodiplostomum, Massoprostatum, Proterodiplostomum, Paradiplostomum,* and *Herpetodiplostomum*).

Separate male and uterine ducts is plesiomorphic according to outgroup comparisons. In two of the four conditions, the paraprostate gland is fused with the male duct, while in the other two cases it is either separate or fused with the uterine duct. Thus, condition (1) is considered plesiomorphic for proterodiplostomes. Conditions (2) and (4) are considered derived from (1) as a result of the fusion of the male and uterine ducts (2) and the loss of connection between the male duct and paraprostate gland (4). Condition (3) is considered derived from (2) as a result of the fusion of the paraprostate gland with the uterine duct rather than the male duct. In this formulation, each of the transformations requires a single structural modification, and no modifications are repeated. Hence, it is the most parsimonious transformation series for the structural components. In addition, this transformation series provides the best fit for the information about the terminal genitalia to the overall phylogenetic hypothesis based on all the characters.

Results and Discussion

We present a phylogenetic tree (Fig. 1) and annotated classification (following the convention of Wiley 1981) with cladistic diagnoses (below) for the new phylogenetic hypothesis for the genera of proterodiplostome digeneans. Numbers following characters in the diagnoses correspond to synapomorphies of the same number on the phylogenetic tree; an asterisk (*) following a character indicates that the character exhibits homoplasy on the tree.

Proterodiplostomidae Dubois, 1936

Diagnosis: Strigeoids with large paraprostate gland (1); with paraprostate and male ejaculatory duct fused, uterus separate (2); paraprostate gland in adults (3); paraprostate gland in metacercariae (4).

Heterodiplostominae Dubois, 1936 incertae sedis, sedis mutabilis

Diagnosis: As above. Parasites of snakes.

Ophiodiplostomum Dubois, 1936, *Heterodiplostomum* Dubois, 1936, *Petalodiplostomum* Dubois, 1936 sedis mutabilis, incertae sedis

Diagnosis: As above.

Proterodiplostominae Dubois, 1936 sedis mutabilis

Diagnosis: Proterodiplostomes with papillose tribocytic organ (5); with vitelline follicles confined to forebody (6). Parasites of crocodilians.

Pseudoneodiplostomini Dubois, 1936 sedis mutabilis

Diagnosis: Proterodiplostomines with inflated genital atrium* (7).

Neelydiplostomum Gupta, 1958

Diagnosis: Pseudoneodiplostomini with terminal genital pores* (8). Parasites of *Gavialis* (Gavialidae).

Pseudoneodiplostomum Dubois, 1936

Diagnosis: Pseudoneodiplostomini with vitellaria in fore- and hindbody* (9). Parasites of *Crocodylus* and *Osteolaemus* (Crocodylidae: Crocodylinae).

Pseudocrocodilicolini Byrd & Reiber, 1942 sedis mutabilis

Diagnosis: Proterodiplostomines

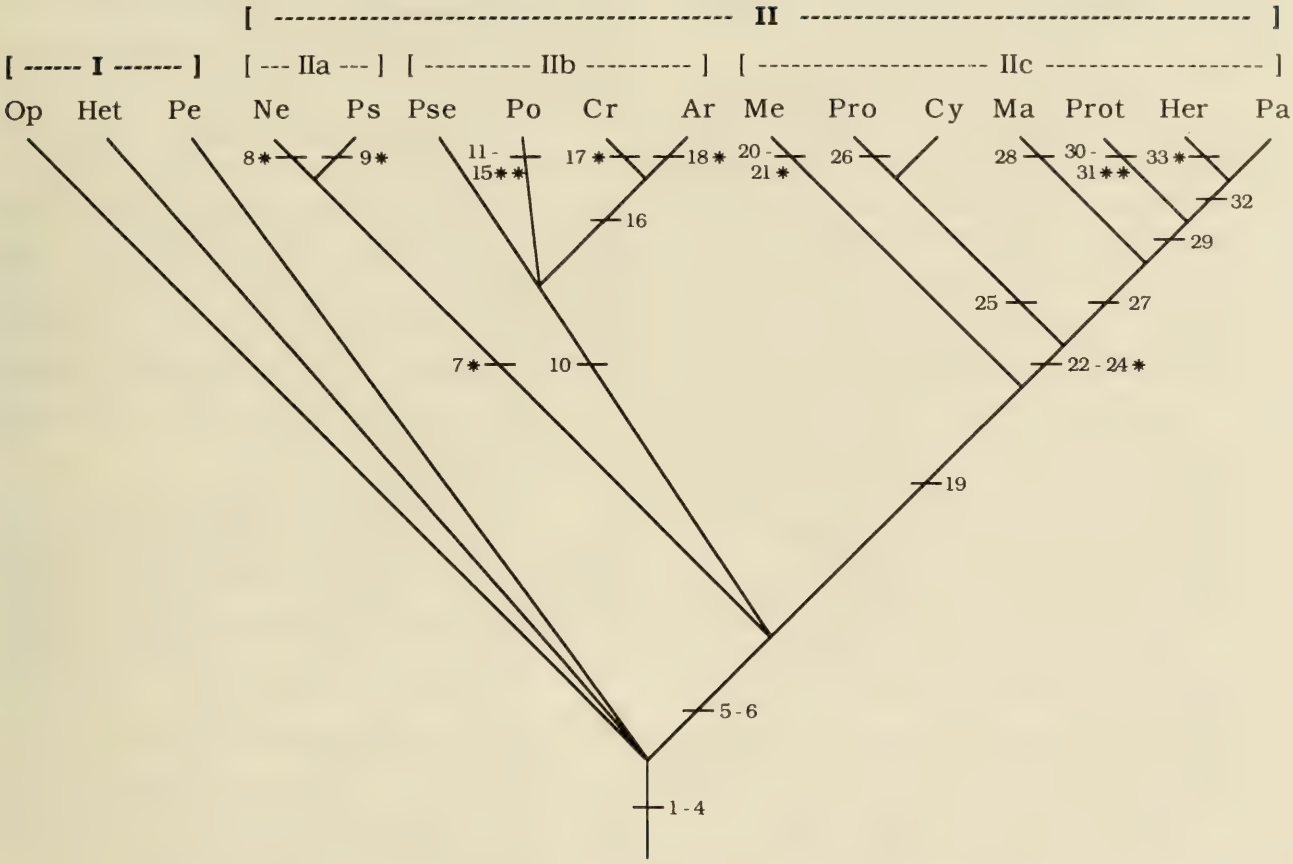

Fig. 1. Phylogenetic tree for genera of Proterodiplostomidae. I = Heterodiplostominae; II = Proterodiplostominae; IIA = Pseudoneodiplostomini; IIB = Pseudocrocodilicolini; IIC = Proterodiplostomini. Op = *Ophiodiplostomum*; Het = *Heterodiplostomum*; Pe = *Petalodiplostomum*; Ne = *Neelydiplostomum*; Ps = *Pseudoneodiplostomum*; Pse = *Pseudocrocodilicola*; Po = *Polycotyle*; Cr = *Crocodilicola*; Ar = *Archaeodiplostomum*; Me = *Mesodiplostomum*; Pro = *Prolecithodiplostomum*; Cy = *Cystodiplostomum*; Ma = *Massoprostatum*; Prot = *Proterodiplostomum*; Her = *Herpetodiplostomum*; Pa = *Paradiplostomum*. Numbers accompanying slash marks on tree indicate synapomorphic traits (identities found in diagnoses in text); asterisks (*) indicate homoplasious characters.

with paraprostate and male ejaculatory duct fused, and uterus fused to that common duct forming a hermaphroditic duct (10). Parasites of *Alligator* (Crocodylidae: Alligatorinae).

Pseudocrocodilicola Byrd & Reiber, 1942 sedis mutabilis, incertae sedis

Diagnosis: With characters of the tribe.

Polycotyle Willemoes-Suhm, 1870

Diagnosis: Crocodilicolini with very small paraprostate gland* (11); with sucker in genital atrium (12); with inflated genital atrium* (13); with many dorsal accessory suckers (14); with Mehlis' gland between ovary and anterior testis (15).

Crocodilicola Poche, 1925

Diagnosis: Crocodilini with extremely small paraprostate gland* (11); with paraprostate fused with uterine duct, and those fused with ejaculatory duct to form a hermaphroditic duct (16); with very small paraprostate gland* (17).

Archaeodiplostomum Dubois, 1936

Diagnosis: Crocodilicolini with vitellaria in fore- and hindbody* (18); with paraprostate fused with uterine duct, and those fused with ejaculatory duct to form a hermaphroditic duct (16).

Proterodiplostomini Dubois, 1936
sedis mutabilis

Diagnosis: Proterodiplostomines with paraprostate not fused with male duct, opening separately into genital atrium (19). Parasites primarily of *Caiman, Melanosuchus* and *Paleosuchus* (Crocodylia: Alligatorinae), occasionally of *Crocodylus* (Crocodylidae: Crocodylinae) or chelonians.

Mesodiplostomum Dubois, 1936

Diagnosis: Proterodiplostomini with genital diverticula (20); with vitellaria in fore- and hindbody* (21). Parasitic in *Melanosuchus.*

Cystodiplostomum Dubois, 1936

Diagnosis: Proterodiplostomini with very small paraprostate gland* (22); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with ventral hindbody constriction (25). Parasitic in *Caiman.*

Prolecithodiplostomum Dubois, 1936

Diagnosis: Proterodiplostomini with small paraprostate gland* (22); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with hindbody constriction around entire body (26). Parasitic in *Caiman.*

Massoprostatum Caballero, 1947

Diagnosis: Proterodiplostomini with small paraprostate gland* (22); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with terminal genital pore (27); with vitellaria confined to hindbody (28). Parasitic in *Crocodylus.*

Proterodiplostomum Dubois, 1936

Diagnosis: Proterodiplostomini with small paraprostate gland* (22); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with dorsal sub-terminal genital pore* (31); with non-eversible genital atrium (29); with vitellaria in fore- and hindbody* (30). Parasitic in *Caiman, Melanosuchus,* and *Paleosuchus.*

Paradiplostomum LaRue, 1926

Diagnosis: Proterodiplostomini with small paraprostate gland* (22); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with terminal genital pore (27); with non-eversible genital atrium (29); with inflated genital atrium (32). Parasitic in *Caiman.*

Herpetodiplostomum Dubois, 1936

Diagnosis: Proterodiplostomini with large paraprostate gland* (33); with gonads close to forebody (23); with gonads close to tribocytic organ (24); with terminal genital pore (27); with non-eversible genital atrium (29); with inflated genital atrium (32). Parasitic in *Caiman, Melanosuchus,* occasionally chelonians.

Discussion

Despite relatively high levels of homoplasy in most characters, the new phylogenetic hypothesis is a more efficient representation of available morphological data than was the hypothesis of Brooks (1979), and incorporates the newest information about the structure of the terminal genitalia. In a revision and new key to the genera of proterodiplostomes, Dubois (1979) considered *Neelydiplostomum* to be a synonym of *Herpetodiplostomum,* but the character evidence presented herein suggests that they are not particularly closely related.

The new hypothesis also indicates a better phylogenetic fit between crocodilian hosts and their digeneans than did the scheme of Brooks (1979). In that earlier hypothesis, *Crocodilicola, Pseudocrocodilicola, Archaeodiplostomum,* and *Polycotyle,* representing those species inhabiting *Alligator mississippiensis,* did not form a monophyletic group, whereas the present hypothesis recognizes the Pseudocrocodilicolini for those genera. In addition, species inhabiting alligatorines other than *Alligator* form the Proterodiplostomini, while those species inhabiting gavials and crocodylines (*Crocodylus* and *Osteolaemus*) form the Pseudoneodiplostomini. The fit between the parasite and definitive host phylogeny would be even stronger if a synapomorphy linking the Pseudocrocodilicolini and Proterodiplostomini were found, but at present we have no such evidence.

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GUIDE TO WESTERN ATLANTIC SPECIES OF *CINACHYRELLA* (PORIFERA: TETILLIDAE)

Klaus Rützler and Kathleen P. Smith

Abstract.—Only a few spicular characters are useful in the determination of *Cinachyrella* (=*Cinachyra* of authors) species once the specimens are preserved. Based on these we recognize four species of this genus in the tropical and subtropical western Atlantic Ocean. *C. alloclada* and *C. kuekenthali* possess two or more size classes of oxeas but only one size class of tetractines, and both lack special accessory spicules. *C. kuekenthali* can be distinguished because the smallest size oxeas are roughened or crenulate. *C. apion* and *C. arenosa* have only one category of oxeote megascleres, but also have rhaphids for microscleres, often organized in trichodragmas; *C. apion* possesses protriaenes in a second, smaller size class, whereas *C. arenosa* adds plagiotriaenes and calthrops to the typical spicule complement. Characteristic specimens, spicules, and special features are illustrated.

The United States continental shelf survey conducted by the Mineral Management Service (Department of Interior) during the early 1980s produced several hundred of the characteristic ball-shaped sponges that are easily classified as belonging to the genus *Cinachyrella* of the family Tetillidae. The necessity of allocating this material to *Cinachyrella* rather than habitually to *Cinachyra* was recently discussed by Rützler (1987) who also reconsidered the status of other genera known in this family. Comparing the newly available large collection with published species descriptions we found that taxonomic revision of the *Cinachyrella* group was needed to provide a practical and reliable manual for non-specialists in need to identify similar material.

Two main difficulties face the identifier of *Cinachyrella,* in fact of most tetillid sponges, particularly preserved ones in small samples: great variation in external characters and spiculation with different habitat conditions and fixation methods; and extreme size range of spicules—from a few micrometers in microscleres to several millimeters in megascleres—which can lead to observation error by loss during standard preparation methods. Also, some spicule types can truly be rare or absent in some specimens and misleading malformations of megascleres occur commonly. Although this paper will not be the cure for all problems associated with identification of these sponges, it can help avoid common mistakes and serve as a practical guide.

Most species of *Cinachyrella* likely to be encountered in the western Atlantic were described by Uliczka (1929), but his paper is confusing because of several inconsistencies between descriptions and illustrations. No one since Uliczka has attempted to reexamine the type material which was thought lost during events of World War II. Luckily, in 1986 most specimens were located in the collection of the Zoological Museum at the Humbold University in Berlin and could be restudied by us. Only one species, *C. kuekenthali,* was not represented, but because it is the most characteristic and best described its validity was never doubted. The following account of recognized *Cinachyrella* species will include reference to the type specimens examined by us.

Material and Methods

Material studied included types borrowed from the Zoological Museum Berlin (ZMB); sponges obtained by the Mineral Management Service (MMS) Continental Shelf Survey off the coasts of South Carolina, Georgia, and southwestern Florida (Gulf of Mexico); and specimens collected by the authors and collaborators in localities ranging from Bermuda throughout the West Indies to Brazil. Observations on live sponges relating to current flow and morphological changes during handling and preservation were made at the National Museum of Natural History's field station on Carrie Bow Cay, Belize.

Ground and polished histological sections were made of formalin-seawater fixed, non-desilicified samples embedded in epoxy resin and spicules were isolated by ashing in boiling nitric acid (for methods refer to Rützler 1978). The great size range of spicules required separate mounts of the very large and the very small ones in order not to miss some types of megascleres and to be able to use high-power objectives to study microscleres. Separation was done in the last alcohol rinse of boiled and washed spicules by gently shaking the test tube and separating its content into a light and a heavy fraction by allowing long (1 h) and short (1 min) sedimentation times. Preparations were made from different regions of a sponge if the resulting spicule complement appeared incomplete.

For spicule dimensions (Table 1), all maximum total lengths were recorded; width measurements were made at the widest point in the case of monaxons (approximately at midlength), and just below the cladomes for tetraxons. Some protriaenes required a second width measurement because they were wider further down the shaft than just below the cladomes. Clad length was measured from the tip to the center point of origin. Only maximum dimension, not thickness, was measured for sigmaspires. Special features and common spicule malformations are shown in previously published photomicrographs (Rützler 1987:figs. 2–5).

Systematic Descriptions

Family Tetillidae Sollas

Tetractinomorph sponges, massive and often globular in shape, with radial skeleton structure, with monaxons, protriaenes, and anatriaenes for principal megascleres, with spinispire-type microscleres, and, in some genera, with unusual accessory spicules.

Genus *Cinachyrella* Wilson, 1925

Globular Tetillidae with porocalices (poriferous pits), without cortex, and without unusual accessory spicules.

Remarks. — *Cinachyra* Sollas was used by previous authors to accommodate the species described below. This genus, however, should remain reserved for species with specialized spicule-reinforced cortex, such as its type, *C. barbata* Sollas (Rützler 1987: 191).

Some accessory spicules, such as plagiotriaenes and calthrops (see the description of *Cinachyrella arenosa* below), are here not considered unusual enough to warrant a different generic placement.

Cinachyrella alloclada (Uliczka, 1929)
Figs. 1–3

Cinachyra alloclada Uliczka, 1929:41, text-figs. 11–15, pl. I, figs. 2, 3; Wiedenmayer, 1977:183, text-fig. 176, pl. 41, figs. 1, 2; van Soest & Sass, 1981:340–341.

Trachygellius cinachyra de Laubenfels, 1936:158, pl. 18, fig. 1.

Cinachyrella alloclada: Rützler, 1987:200, figs. 1d, f; 2a–d; 3a; 5a, b.

Diagnosis. — Orange to yellow reef sponges; globular, up to 100 mm in diameter, with small (3 mm) or large (15 mm) porocalices; with smooth oxeas in two or three size classes, tetractines (pro- and anatriaenes) of only one size, and with sigmaspires of considerable size range (10–23 μm).

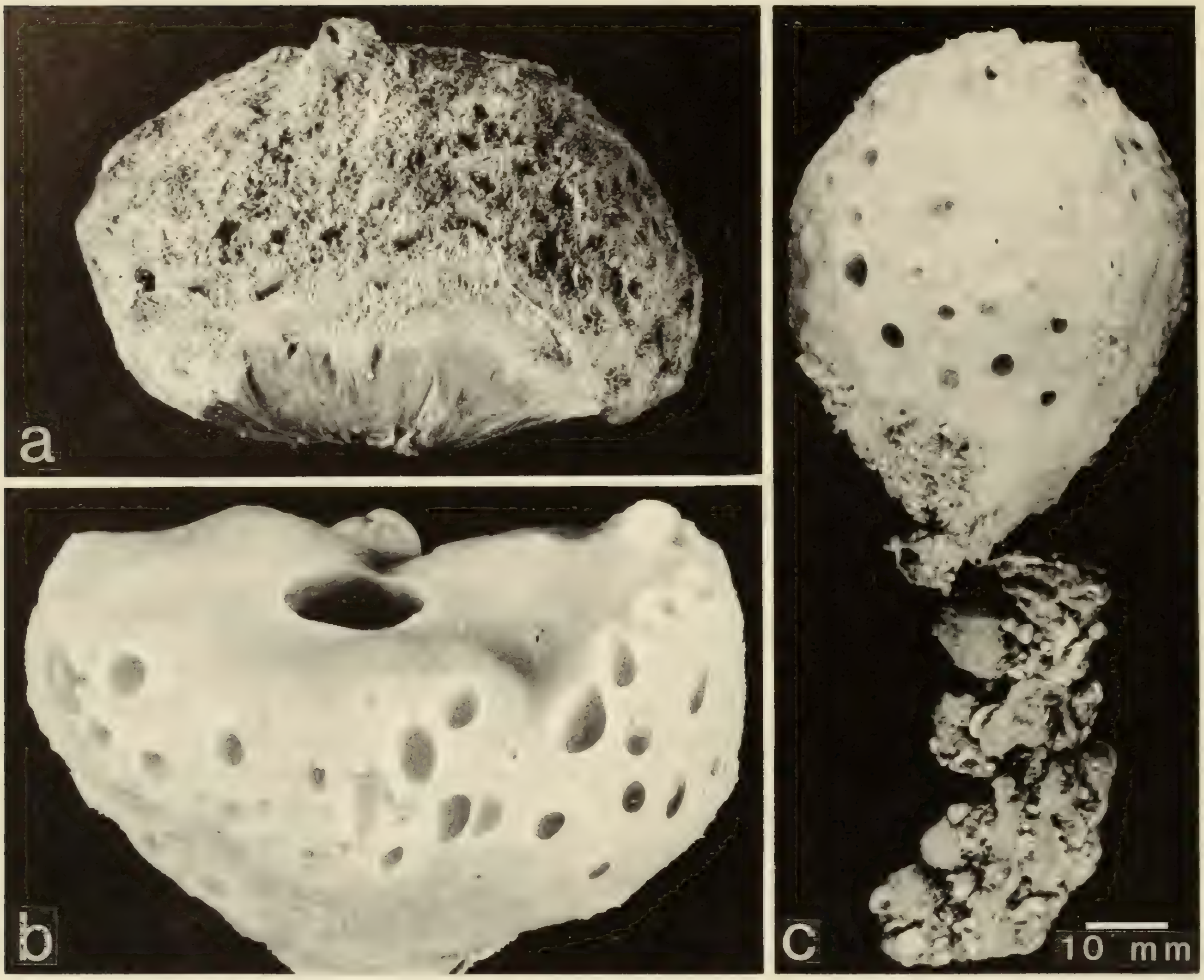

Fig. 1. *Cinachyrella alloclada,* morphology of alcohol preserved specimens: a, High-energy rock pavement, Bimini (Bahamas), 3 m; b, Secondary hard bottom, southwest Florida, 31 m depth; c, Secondary hard bottom, southwest Florida, 56 m. (Scale applies to a–c.)

Color.—Bright orange or yellow in life, except where surface is obscured by sediment; paler colored interior. Preserved specimens turn tan or gray in alcohol.

Shape, size, and consistency (Fig. 1).—Basically globular. Hemispherical specimens occur in high-energy environments, pear-shaped sponges may be the result of calm-water habitats with high sedimentation rate. Large (over 80 mm), old specimens can attain massive cake shape with broad attachment area. Commonly, specimens are 60 mm in diameter and 40 mm in height but some reach 100 × 70 mm. The hispid surface is pitted by numerous porocalices, circular or oval, ranging in some specimens 1–6 mm in diameter and 3–8 mm in depth, in others 5–20 × 3–20 mm. Oscula are few (three to five), ca. 5 mm in diameter and often slightly raised above the sponge surface; they are always contracted in fixed specimens. Consistency of the sponge is very firm.

Spicules (Fig. 2, Table 1).—Smooth oxeas can usually be discerned in three size categories averaging 3500 μm, 1800 μm, and 355 μm in length; one of the smaller classes may be absent in some samples. Many of the large oxeas show malformations, such as a sharp kink near one end, 70–1000 μm (average 260 μm) from the point; other tip modifications result in styloid, substyloid, and anisostrongylote forms. Protriaenes (some modified to prodiaenes) and ana-

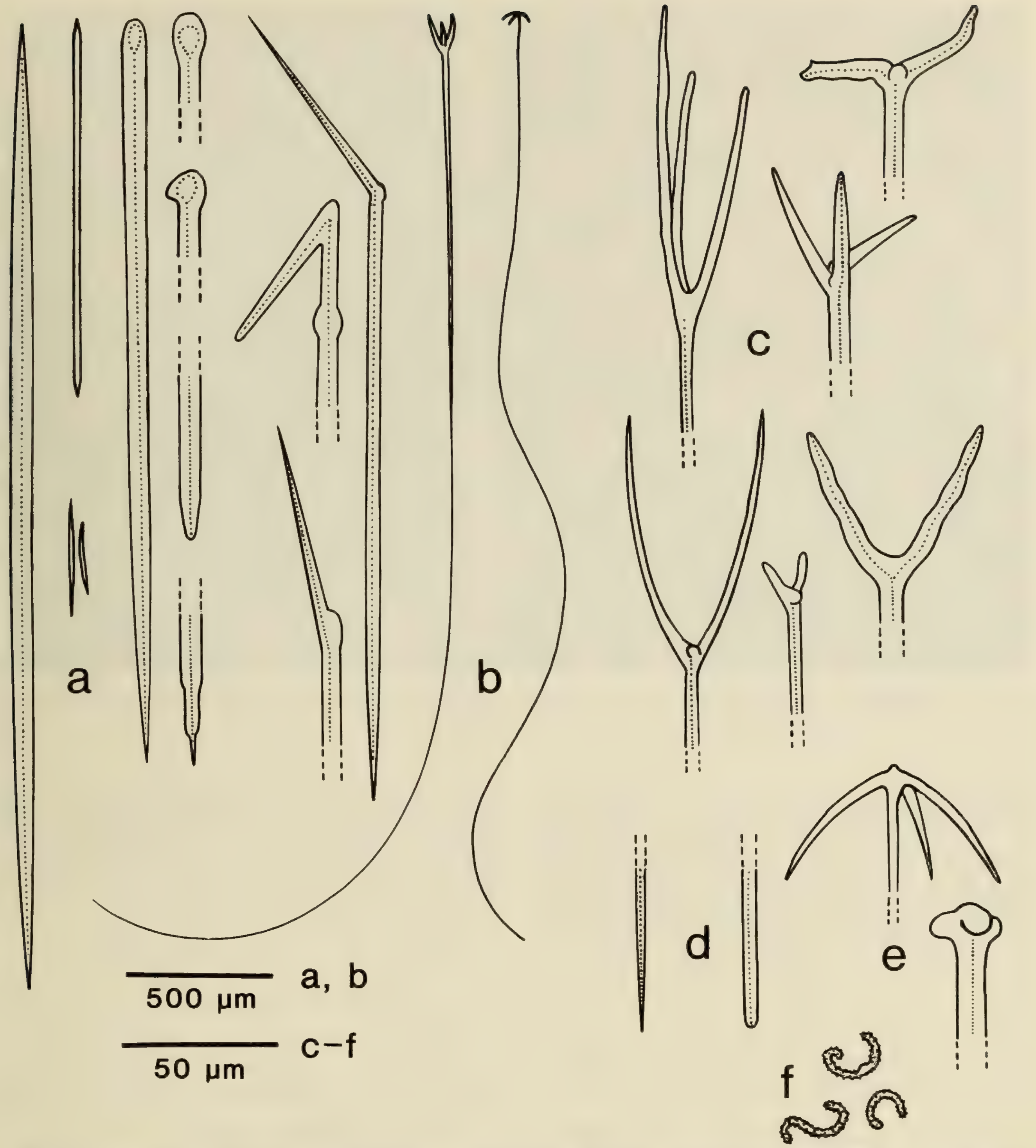

Fig. 2. *Cinachyrella alloclada,* spiculation: a, Oxeas (large, medium, small) and modifications; b, Tetractines; c, Protriaene cladomes and modifications; d, Protriaene shaft points; e, Anatriaene cladome and modification; f, Sigmaspires.

triaenes occur in only one size, similar in length to the largest oxeas but with considerably thinner shafts. Protriaenes are the most common tetractines in most specimens but in a few they are almost entirely replaced by anatriaenes. Variations include prodiaenes (one of the three clads reduced) which can make up almost half the complement of this spicule type, rhabds with rounded points or with thickest diameter at midlength rather than next to the cladome, and clads that are crooked, diverging in an unusually wide angle (as much as 120°), or reduced to knobs. Anatriaenes in some

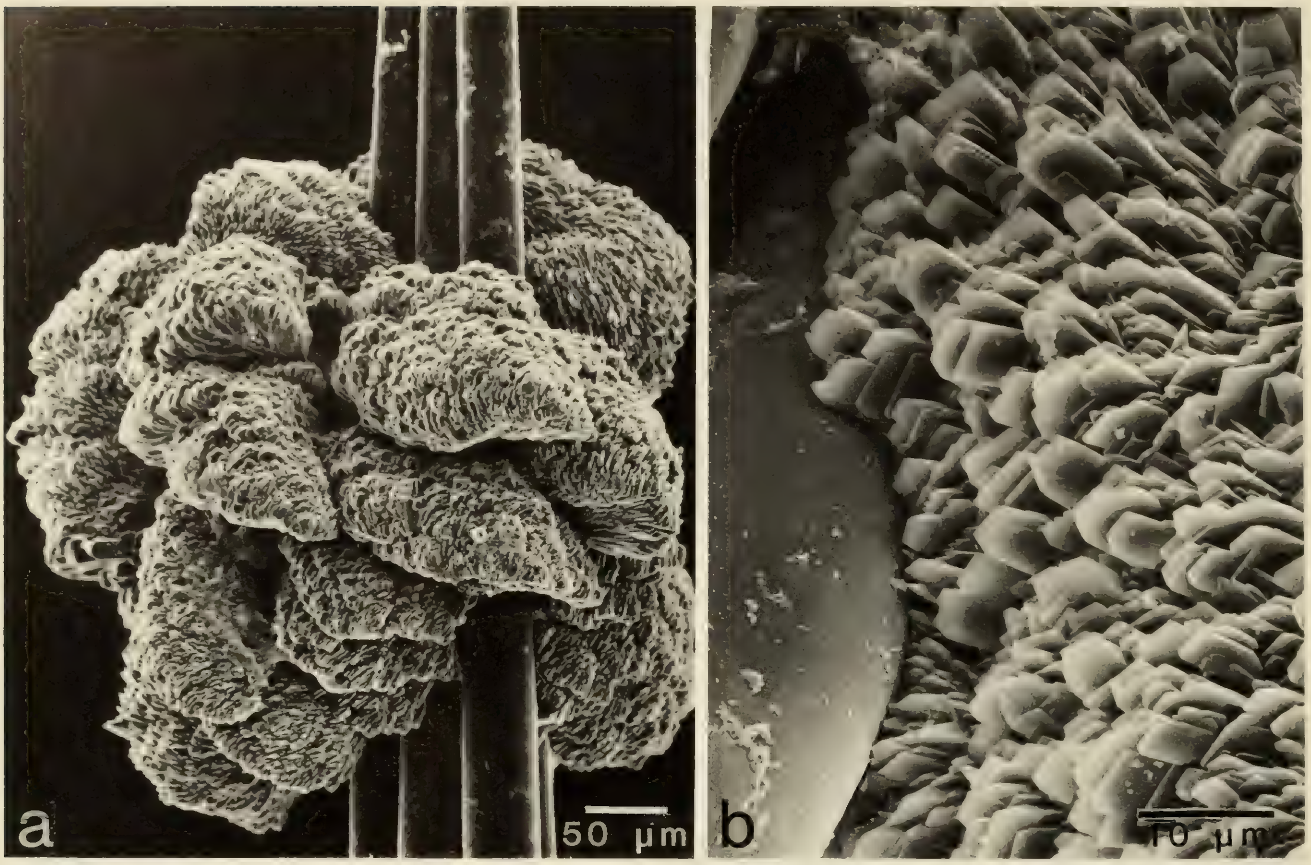

Fig. 3. *Cinachyrella alloclada,* calcareous precipitates: a, Granule enveloping bundle of large oxeas; b, Crystalline granule structure contrasted by smooth siliceous spicule surface.

specimens can be very rare or missing entirely, in others they outnumber the protriaene forms; the clads are usually thin and delicate, but in some material they are stubby, or reduced to mere knobs. Sigmaspires measure 14.3 µm on average and are c- or s-shaped, twisted into third dimension; they are microspined and at times with centrotylote swelling.

Microscopical anatomy.—The basic

Table 1.—Ranges (length, or length × width) and means (*italics*) of spicule dimensions (in µm) of four western Atlantic *Cinachyrella* species. Lengths are overall measurements, widths were measured at the widest part for monaxons, at base of cladomes for tetraxon rhabds. (NP = not present.)

Species	Number of specimens analyzed	Oxeas			Protriaenes, -diaenes 1		Plagiotriaenes
		1	2	3	Rhabds	Clads	Rhabds
C. alloclada	29	1500–5900	900–2800	100–950	2400–6500	14–250	NP
		3500 × 50	*1800 × 13*	*355 × 5.4*	*4200 × 10.7*	*127*	
		20–65	1–20	2.5–8.0	4–20		
C. kuekenthali	13	2500–4100	1300–2700	70–200	400–4600	20–130	NP
		3200 × 35	*2200 × 8*	*135 × 2.9*	*3800 × 11.3*	*50*	
		14–40	3–10	2–4	5–18		
C. apion	16	3500–4600	NP	NP	1800–8000	25–230	NP
		4100 × 41			*3500 × 8.3*	*115*	
		35–45			4–10		
C. arenosa	19	2900–5500	NP	NP	1900–4400	40–200	620–2000
		3900 × 48			*2900 × 10.9*	*110*	*1650 × 17*
		35–60			5–26		12–20

structure of these sponges is revealed by sections perpendicular to the surface. Oxeas and styloids occur in staggered bundles radiating toward and beyond the ectosome, in places alternating with tetractines, cladomes facing outward; styles seem always positioned with the rounded end directed toward the surface; sigmaspires are scattered throughout the tissue. The ectosome is 0.5–1.0 mm thick and separated from the choanosome by water-carrying spaces. Spherical choanocyte chambers measure 30 μm in diameter. Large (20 μm), microgranular, strongly safranin-O staining cells are common and particularly concentrated in the outer ectosome and in clusters among the choanocyte chambers. There are also conspicuous, rounded, brownish bodies, 150–300 μm in diameter, detectable only in samples not treated by acid. These features were observed by us in a number of specimens but were studied particularly in specimens USNM 30347 from Bimini and USNM 42441 from southwestern Florida. These structures are crystalline, show double refraction in polarized light, dissolve in acid, and are therefore presumed to be of calcareous substance. Embedded spicules indicate that they were formed inside, perhaps even secreted by the sponges (Fig. 3).

Distribution and ecology.—Specimens are found as far north as Cape Hatteras, North Carolina, off South Carolina, in the northern Bahamas, in the Florida Keys including the Dry Tortugas, and off the west coast of southern Florida. These sponges occur in coral habitats and on rock pavements or secondary hard bottoms between 3 m and 80 m.

Redescription of holotype.—ZMB 4921 from the Dry Tortugas, Florida, is semiglobular (apparently torn from hard substrate), 60 mm in length, 50 mm in width, 30 mm in height and of very firm consistency. The surface is bristly. The porocalices are primarily located along sides, 1–2 mm (1.5 mm average) in diameter, mostly in fairly close distance (2–5 mm) from each other. Three oscular mounds (oscula contracted) are on top of the specimen and are 5 mm high. Spicule preparations (from tissue near two existing cuts in the specimen and from the damaged attachment area) revealed paucity of all tetractines, particularly anatriaenes. Description and figures agree well with those of the original author (Uliczka 1929).

Other material studied.—USNM 32664, off North Carolina, 100 m; USNM 30472, off South Carolina, 18 m; USNM 41937, off Southwest Florida, 17 m; USNM 42441, off Southwest Florida, 58.5 m; USNM 22433 (holotype of *Trachygellius cinachyra* de Laubenfels), Dry Tortugas, Florida, 70 m;

Table 1.—Extended.

Plagiotriaenes		Protriaenes, -diaenes 2		Anatriaenes			
Clads	Calthrop rays	Rhabds	Clads	Rhabds	Clads	Raphides	Sigmaspires
NP	NP	NP	NP	2200–4000 *3200 × 8.3* 3–14	13–130 *77*	NP	10–23 *14.3*
NP	NP	NP	NP	1900–6000 *3700 × 6.3* 3–10	20–60 *39*	NP	12–24 *16.3*
NP	NP	400–1800 *1350 × 2.3* 1–4	8–90 *28*	1800–3500 *2900 × 4.6* 3–5	25–60 *40*	200–270 *244 × <1*	12–16 *13.4*
230–550 *265*	160–260 *204 × 23* 18–30	NP	NP	900–5300 *2600 × 8.5* 5–18	10–100 *60*	100–250 *220 × <1*	5–20 *12.8*

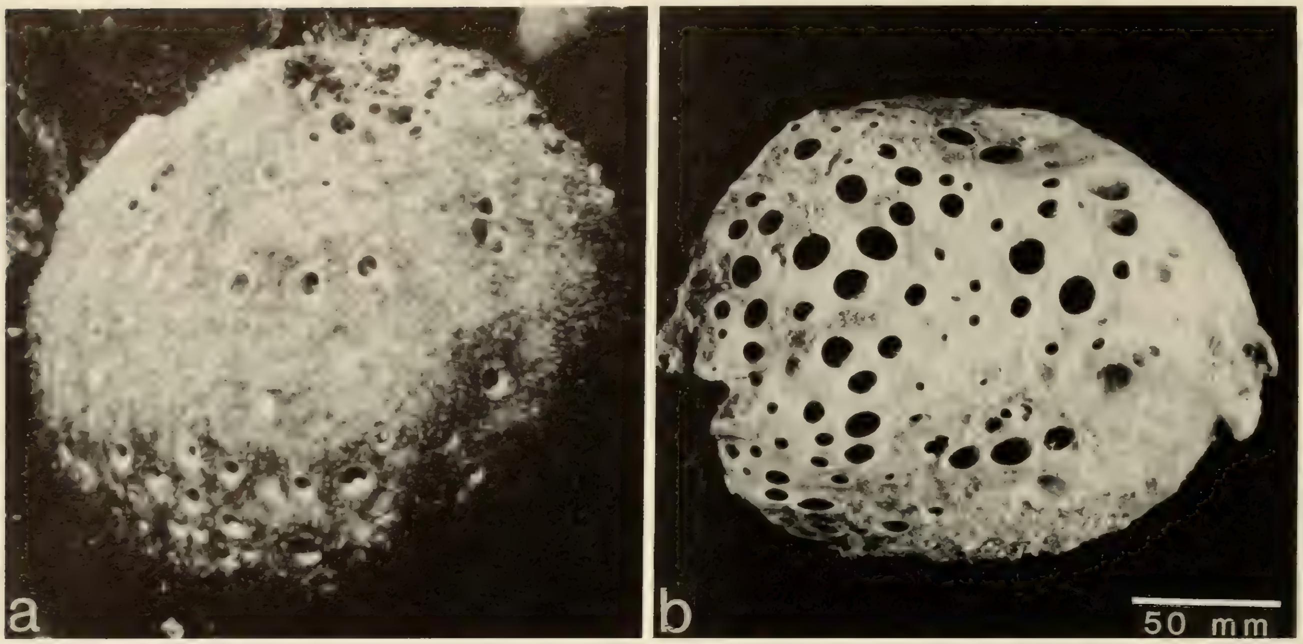

Fig. 4. *Cinachyrella kuekenthali,* morphology: a, Live in situ, patch reef near Carrie Bow Cay, Belize, 4 m; b, Alcohol preserved after initial freezing, off Pará River, Brazil, 68 m. (Scale applies to a, b.)

USNM 30347, Bimini, Bahamas, 7.5–9 m; and 23 uncataloged specimens from the MMS Continental Shelf Survey.

Remarks.—*Trachygellius cinachyra* de Laubenfels (1936:158) is a member of this species; the diagnosis by the original author was flawed by poor preparation technique. On the other hand, *C. alloclada* described from Bermuda (Rützler 1986:126; also, *C. cavernosa* sensu de Laubenfels 1950) must be reexamined; all specimens available to us from that location belong to *C. apion.*

Cinachyrella kuekenthali (Uliczka, 1929)
Figs. 4, 5

Cinachyra kuekenthali Uliczka, 1929:43, text-figs. 16–21, pl. I, fig. 4; Wiedenmayer, 1977:185, text-fig. 177, pl. 41, figs. 3, 4; van Soest & Sass, 1981:340–341; van Soest & Stentoft, 1988:42, fig. 19.

Cinachyra schistospiculosa Uliczka, 1929: 45, text-figs. 27–30, pl. I, fig. 6.

Cinachyrella kuekenthali: Rützler, 1987: 200, figs. 2f, 5c.

Diagnosis.—Orange to brownish orange reef sponges; subspherical, reaching 200 mm in diameter, with small (5 mm) porocalices; with three size classes of oxeas, the smallest one crenulate; with one size class of tetractines (pro- and anatriaenes); and with large sigmaspires (16.3 μm average).

Color.—The surface color of the live sponge is orange or yellow orange, the interior is rich yellow. Brown-appearing specimens are coated by a film of filamentous algae or cyanobacteria, such as *Schizotrix mexicana.* Specimens preserved in alcohol appear gray or light tan.

Shape, size, and consistency (Fig. 4).—Subspherical, globular, or erect egg-shaped. Specimens of 150–200 mm diameter are common, placing this among the largest species of the genus. Characteristically, these sponges have a more or less pronounced depression on top in which porocalices are high in density. The surface is moderately hispid. Porocalices are numerous, 1–5 mm in diameter, 5 mm deep; only in some deep-water forms (below 30 m) they were noted as big as 10 mm across. Oscula are comparatively few and clearly separate from porocalices, 1–5 mm in diameter in life, always contracted in preserved material forming wart-like structures. The consistency of these sponges is elastic but firm.

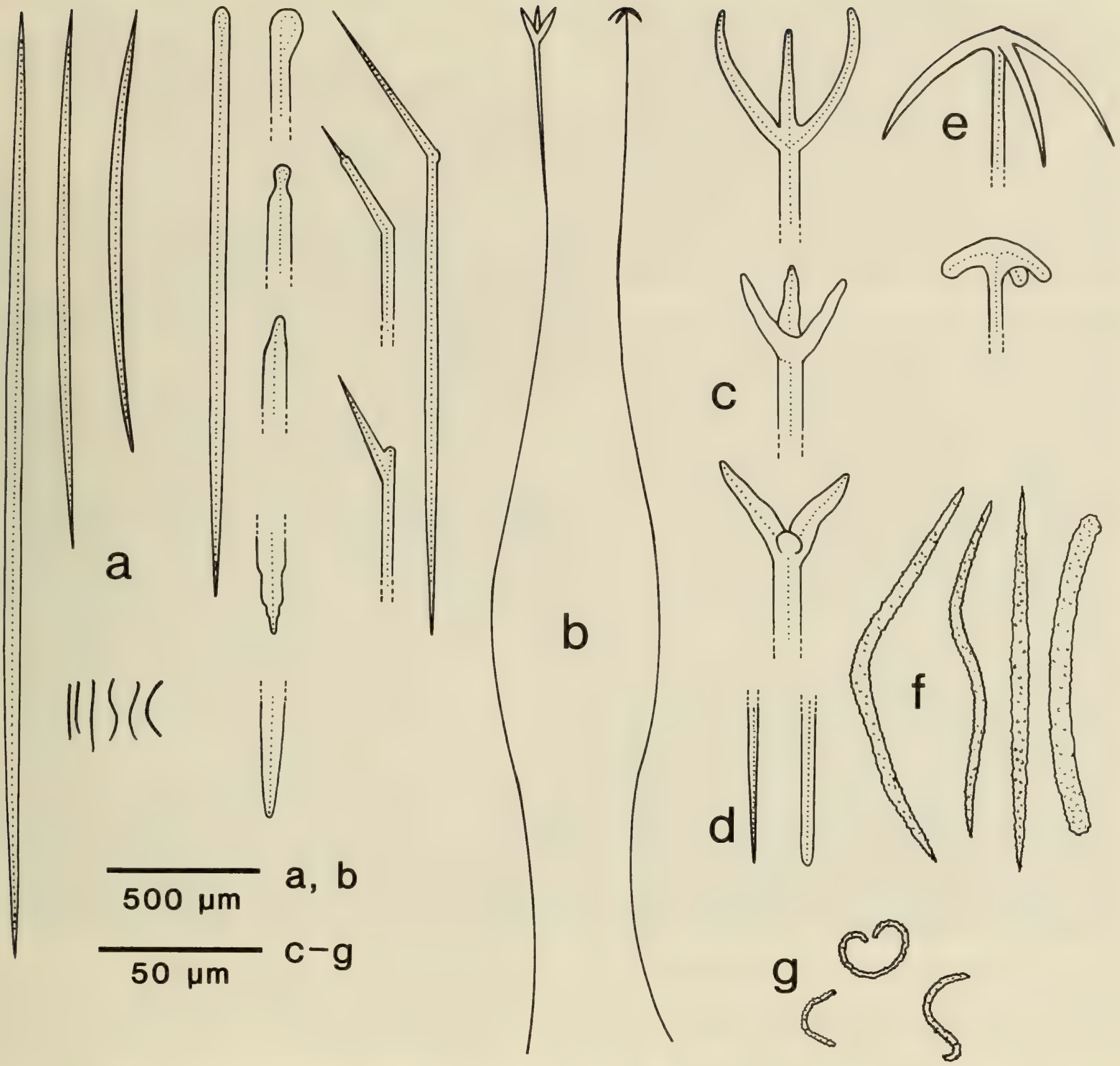

Fig. 5. *Cinachyrella kuekenthali,* spiculation: a, Oxeas (large, medium, small) and modifications; b, Tetractines; c, Protriaene cladomes and modifications; d, Protriaene shaft points; e, Anatriaene cladome and modification; f, Smallest (crenulate) category oxea enlarged; g, Sigmaspires.

Spicules (Fig. 5, Table 1).—Oxeas in three size categories, two smooth (3200 μm and 2200 μm in average length), the third and smallest one (135 μm long) microspined or crenulate (use high-resolution microscopy, possibly phase contrast, to ascertain this structure). Variations of the larger oxeas include kinked, styloid, and asymmetrically strongylote forms; the microxeas, commonly straight and fusiform, can display strongly center-bent, s-shaped, even strongylote forms. Protriaenes are very common and of one size class. They have short, stout clads, one of which may be reduced to a knob, or missing (prodiaene, numbering about half the population of protriaenes). Their rhabds may have rounded points or increase at midlength to greater diameter (15 μm) than at the cladome base (6.3 μm average). Anatriaenes are less common but not rare; they have very slender clads except for a few reduced, crippled forms. Sigmaspires are thin and large compared to the other species (over 16 μm), c- and s-shaped, and microspined.

Microscopical anatomy.—The histological structure is identical to that of the previous species except that the ectosomal region in these large sponges is about 2.5 mm thick and reinforced by conspicuous surface sediments and commonly covered by a layer of intertwined filamentous oscillatorians. No special calcareous grains were found in the choanosome.

Distribution and ecology.—Locations of material examined by us range from off North Carolina (34° northern latitude) throughout the West Indies to northeastern Brazil (1° northern latitude), including the Bahamas, southwestern Florida, Puerto Rico, Jamaica, Belize, and Colombia. These sponges are characteristic of medium-energy coral reef environments in 4–20 m depth but are also common on hard bottoms down to 100 m.

Holotype.—Uliczka's specimen from St. Thomas (Virgin Islands) was unavailable for examination and is presumed lost. We are therefore establishing specimen USNM 31491 as neotype. The alcohol-preserved sample constitutes about 20% of a 7 cm diameter subspherical sponge which was brilliant red orange in life. It shows numerous 1–2 mm porocalices as well as a few oscular openings. The characteristic small, crenulate oxeas measure 70–139 × 2–3 μm. It was collected by one of us (KR) on 29 March 1967 near the original type locality off St. John, Virgin Islands, in 16 m depth.

Other material studied.—USNM 33559, off North Carolina, 100 m; USNM 42521, off southwest Florida, 31.5 m; USNM 30348, Bimini, Bahamas, 20 m; USNM 30138, Puerto Higuera, Puerto Rico, 6–8 m; USNM 42431, Discovery Bay, Jamaica, 6–10 m; USNM 32323, Lighthouse Reef, Belize, 6–10 m; USNM 42433, Carrie Bow Cay, Belize, 4 m; USNM 31983, Colombia, 22 m; USNM 42427, off Amazon River, Brazil, 63 m; and 3 uncataloged specimens from the MMS Continental Shelf Survey.

Remarks.—Uliczka's (1929) description and figures leave no doubt about the validity of this species although he overlooked the microspination on the small size class of oxeas, a feature first pointed out by Wiedenmayer (1977). The latter author, in turn, did not find anatriaenes which are fairly common in our material. We examined the type specimen of *Cinachyra schistospiculosa* Uliczka (ZMB 4906) and found the characteristic microspined microxea, confirming our earlier suspicion that it is conspecific with *Cinachyrella kuekenthali* (van Soest & Sass 1981, Rützler 1987). The "split" oxeas reported by Uliczka (1929) are an artifact commonly observed in spicule mounts of these sponges, that is, two or three very thin hair-like spicules (raphids, broken rhabs of tetractines, etc.) of equal length are bundled together in the center, appearing like a homogenous monactin, but are slightly separated toward the ends.

Cinachyrella apion (Uliczka, 1929)

Figs. 6, 7

Cinachyra apion Uliczka, 1929:43, text-figs. 16–21, pl. I, fig. 4; van Soest & Sass, 1981: 340–341.

Cinachyra rhizophyta Uliczka, 1929:38, text-figs. 1–10, pl. I, fig. 1.

Cinachyra cavernosa (Lamarck) sensu de Laubenfels, 1950:128, text-fig. 56, pl. II, fig. 7.

Cinachyra subterranea van Soest & Sass, 1981:337–341, text-fig. 4, pl. II, fig. 2.

Cinachyrella apion: Rützler, 1987:200, figs. 2g; 3b–g; 4a, c; 5d, e.

Diagnosis.—Yellow or light gray calm-water lagoon sponges; globular, up to 100 mm in diameter, with small (3 mm) porocalices, often with surface buds; with one size class of oxeas and anatriaenes, two size classes of protriaenes, and with raphids and small (13 μm) sigmaspires.

Color.—Clear yellow or light gray in life, tan or gray in alcohol.

Shape, size, and consistency (Fig. 6).—Small (10–40 mm) specimens are spherical, larger ones (50–100 mm) are oval or lumpy

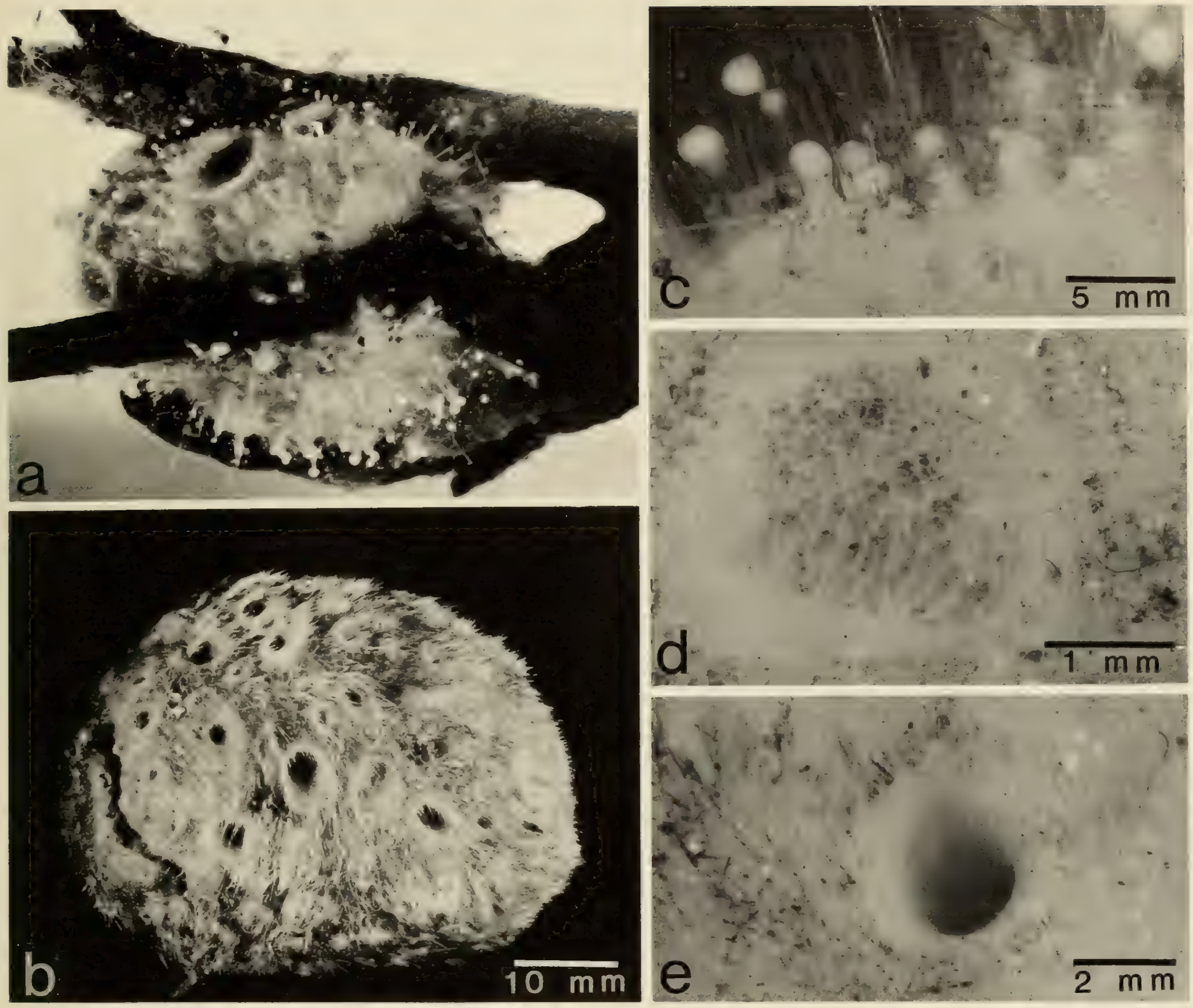

Fig. 6. *Cinachyrella apion,* morphology: a, Live specimen attached to alga *Avrainvillea,* Twin Cays mangrove pond, Belize, 0.3 m; b, Alcohol-preserved specimen, same location as a; c, Buds, close-up of specimen similar to a; d, Porocalyx, close-up of specimen similar to a; e, Osculum, close-up of specimen similar to a. (Scale in b also applies to a.)

massive; the latter may have derived from fusion of two or more adjacent specimens, possibly originating from liberated buds. The surface is strongly hispid, even furry from protruding hair-like spicules, and studded with 0.5–2 mm buds. Procalices are abundant but small, rarely exceeding 3 mm in diameter; they can be shallow (0.5 mm) or more than 3 mm deep. Oscula are rare, 2–3 mm in diameter, and flush with the sponge surface. The consistency of the sponges is soft and compressible.

Spicules (Fig. 7, Table 1).—Large oxeas occur in one size class and include common styles and few subtylostyles and strongyles. Protriaenes are of two size classes, the larger one almost as long as the oxeas, the smaller one less than half as long and less than one-third as thick. Large protriaenes can have strongly crippled clads and rhabds that are thickest at midlength (14–20 μm) rather than at the clad base and often end in rounded points; prodiaene forms make up almost half the number. Small protriaenes and prodiaenes occur in equal proportion. Anatriaenes have slender, curved rays, some end in rounded shaft tips. They are common in most specimens. Microscleres include raphids, some arranged in bundles (trichodragmata), and small (13.4 μm), thin sig-

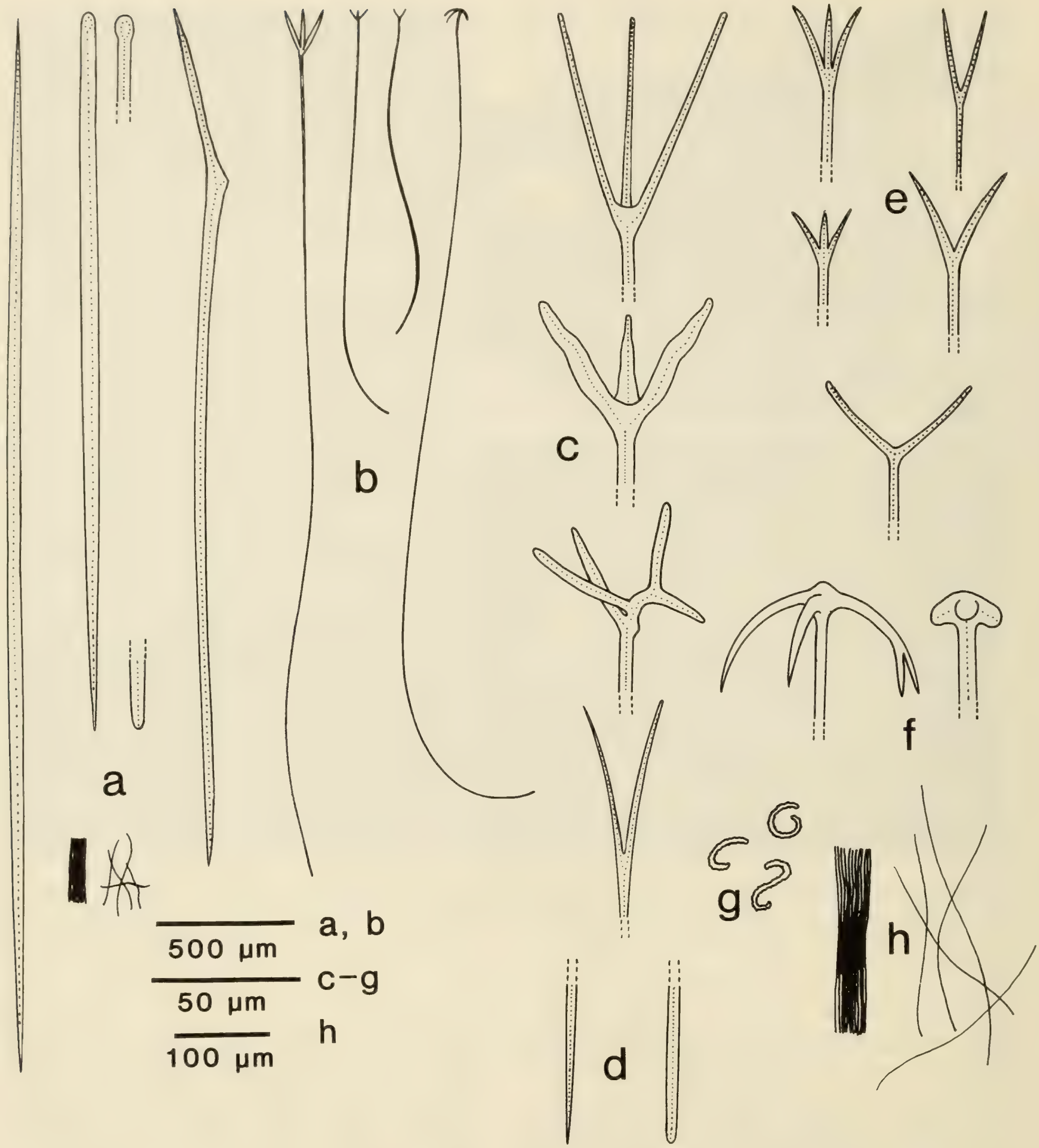

Fig. 7. *Cinachyrella apion,* spiculation: a, Oxeas and modifications, raphids; b, Tetractines in two size classes; c, Protriaene 1 cladomes and modifications; d, Protriaene 1 shaft points; e, Protriaene 2 cladomes and modifications; f, Anatriaene cladome and modification; g, Sigmaspires; h, Raphids enlarged, some bundled into a trichodragma.

maspires that vary considerably in shape, forming s-, c-, and o-figures.

Microscopical anatomy.—Ground epoxy sections show clearly that the second, smaller category of protriaenes occurs primarily in and around the porocalices. Choanocyte chambers measure about 25 μm in diameter, rarely as much as 30 μm. Histological variety, even in well fixed material, is generally poor. Brownish, double refracting spherical inclusions of the kind described for *Cinachyrella alloclada* are common in some specimens; they occur in the 20 μm as well as 150–300 μm size class. There are also grayish spherical inclusions, not double refracting and of unknown origin, seen in material from Belize mangroves; they measure 20 μm.

Distribution and ecology.—This species is common in shallow calm-water and inshore environments but it has generally been overlooked by previous authors because of its small size and cryptic occurrence. Our material indicates a distribution from offshore North and South Carolina, to Bermuda, southwestern Florida, Bahamas, Virgin Islands, and Belize. The recorded depth range is from 0.3 m to almost 60 m. In Bermuda we collected it in the intertidal from overturned rocks and from mangrove roots and inside shallow caves in inshore saltwater ponds and lakes. In Belize we found it most common in mangrove creeks and ponds, attached to red mangrove stilt roots, peat banks, and *Avrainvillea* algae stipes. One record from Grand Bahama is from 20 m depth, 100 m into a large limestone cave.

Redescription of holotype.—ZMB 4911 from St. Thomas, Virgin Islands, has the shape of an erect pear, 55 mm tall, 35 × 40 mm in diameter. It is firm, elastic, with bristly surface. No oscula are clearly discernible except for two apical openings, 2 mm and 4 mm in diameter and flush with the surface, which are in connection with large canals; other holes may be punctures. Porocalices are mostly collapsed but still recognizable from the dense lining of small protriaenes. No buds are visible on the surface but these could have been removed by handling and wrapping in cotton. Generally, the description of spicules by the original author (Uliczka 1929) is accurate but he neglected to figure the smaller category of protriaenes and he overlooked the raphids altogether.

Other material studied.—USNM 32652, off North Carolina, 34 m; USNM 33109, off South Carolina, 33 m; USNM 33249, off South Carolina, 17 m; USNM 42413, Hungry Bay, Bermuda, 1 m; USNM 42416, Walsingham Pond, Bermuda, 4 m; USNM 42417, Ferry Reach, Bermuda, 1 m; USNM 42422, Sarasota Bay, Florida, 9–11 m; USNM 33698, Grand Bahama, Bahamas, 20 m; USNM 42428 & 42429, Twin Cays, Belize, 1 m; and 6 uncataloged specimens from the MMS Continental Shelf Survey.

Remarks.—Examination of the holotype of *Cinachyra rhizophyta* Uliczka (1929; ZMB 4910) confirmed earlier suspicions (van Soest & Sass 1981, Rützler 1987) that this is a synonym of *Cinachyrella apion.* This specimen is not well preserved, it is badly contracted and torn, but a number of buds are still preserved in one area of the surface and the spiculation shows all characteristic features. Restudying preparations made from the type of *Cinachyra subterranea* van Soest & Sass (1981) we found a few small prodiaenes and raphids indicating that this sponge belongs to *Cinachyrella apion* rather than *C. alloclada* as previously assumed (Rützler 1987); this view is also consistent with records of distributional ecology for *C. apion.*

Cinachyrella arenosa
(van Soest & Stentoft, 1988)
Figs. 8, 9

Cinachyra arenosa van Soest & Stentoft, 1988:45, text-fig. 20, pl. VI, fig. 4.

Diagnosis.—Whitish to orange(?) deep-reef sponges; globular to ovoid, not more than 45 mm in diameter, with relatively large (5–10 mm) porocalices; with large oxeas, protriaenes and -diaenes (all of one size class), with robust accessory plagiotriaenes and calthrops, and with raphids and small (13 μm) sigmaspires.

Color.—We observed no live material. Based on alcohol-preserved specimens which range from gray (dominated by protruding spicules) to tan and reddish brown, we assume that small live sponges are gray,

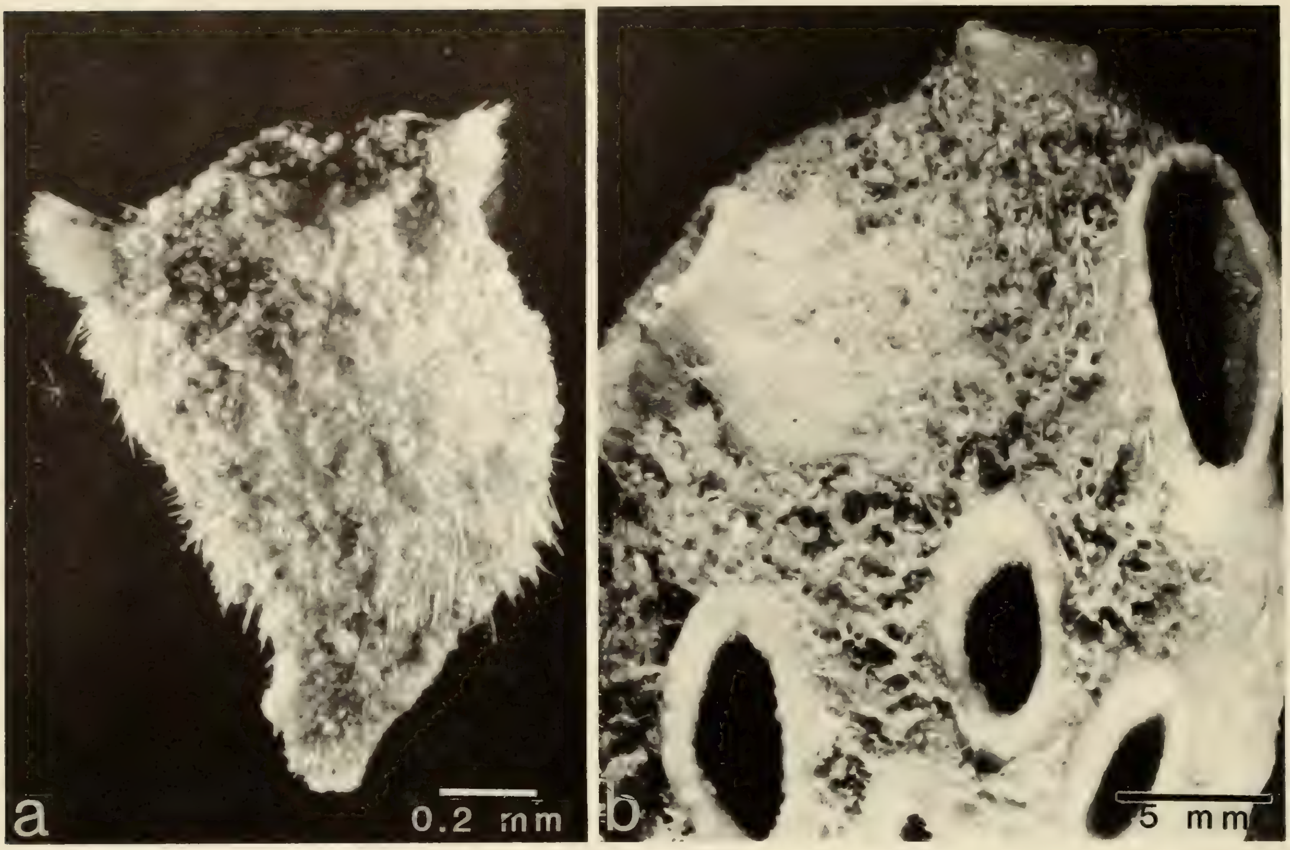

Fig. 8. *Cinachyrella arenosa,* morphology: a, Holotype, dry ZMA 5266, Barbados, 153 m (photo courtesy of R. W. M. van Soest); b, Alcohol-preserved specimen from southwest Florida, 44 m.

larger ones vary from yellow to orange. The color may often be obscured by sediments trapped between exposed spicules.

Shape, size, and consistency (Fig. 8).—Small specimens (5–15 mm tall) are ovoid erect, some are stalked; larger sponges are globular or subglobular and reach 45 mm in maximum dimension. The surface is usually hispid from protruding spicules which may trap large amounts of sand and other sediments. Porocalices are few (2–6) and mostly large (5–10 mm) compared to body size; they are elevated and many are surrounded by a fleshy rim or a collar of spicules. All observed oscula were contracted, located on top of cone-shaped protuberances. Consistency (alcohol material) is soft (small specimens) to moderately firm.

Spicules (Fig. 9, Table 1).—All spicules occur in one size class, with a few exceptions noted below. Oxeas are large and smooth; only a few are misformed to styles or with a kink near one tip. Protriaenes and prodiaenes (which occur in about equal proportions) display a considerable variety in shapes. They can have unusually short and stout rays, rays that open outward in a wide angle (45° from the rhabd axis), rhabds that are thickest at midlength rather than next to the cladome, and those that end rounded rather than pointed. Two (of 19) specimens studied had porocalices adorned by a number of very small protriaenes or -diaenes (900 × 3 μm overall, 40–60 μm clads); these were too rare and untypical to be included in Table 1. Plagiotriaenes are common and conspicuous. Despite their variation in shape and cladome angles they are always distinct from protriaenes (even crippled ones) by having much shorter (half the length) rhabds and much longer (three times the length) clads. In regular cladomes, the clad angle is about 45° to the rhabd axis, directed straight forward, but many are angulate, crooked, distally recurved, or otherwise deviating from the typical symmetry. Regularly co-occuring with plagiotriaenes is a related spicule type, the calthrop, which

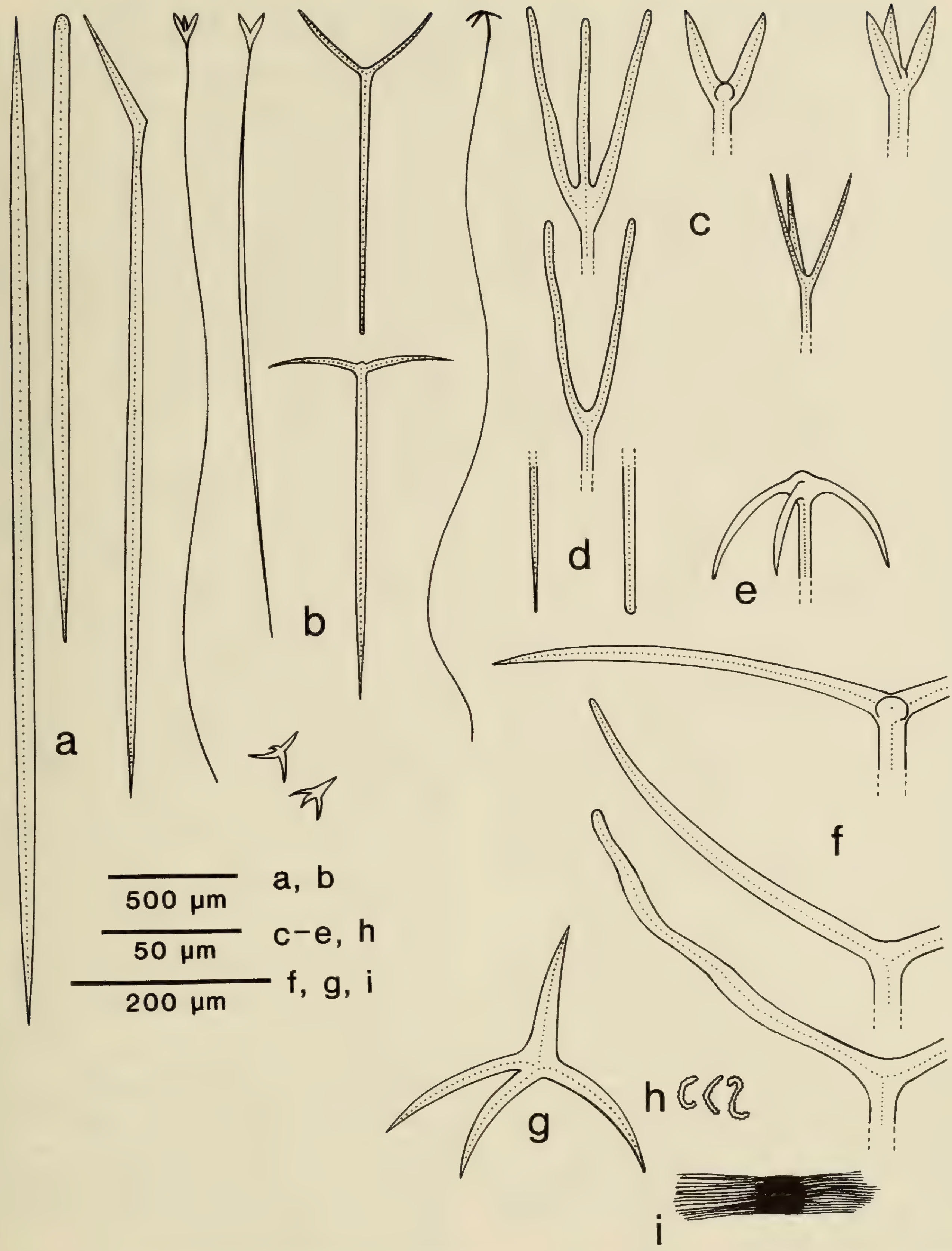

Fig. 9. *Cinachyrella arenosa,* spiculation: a, Oxea and modifications; b, Tetractines; c, Protriaene cladomes and modifications; d, Protriaene shaft points; e, Anatriaene cladome; f, Plagiotriaene cladomes; g, Calthrops; h, Sigmaspires; i, Raphids bundled in trichodragma.

is characterized by four equal rays that radiate from a common center. The fifth type of megasclere are anatriaenes with slender, regularly curved clads. They show little variation in shape. In some sponges they occur in numbers equal to protriaenes, but in many they are dominating the latter ten to one or more. Microscleres include raphids, often forming trichodragmata, and small (12.8 μm), regular (mostly c-shaped) sigmaspires.

Microscopical anatomy.—None of the available specimens were fixed for histological examination. Choanocyte chambers could be measured as 25 μm in diameter and it is apparent that histological diversity in this material is low. A ground, polished section revealed that the small category of protriaenes detected in abundance in one specimen (see comment above) was indeed implanted around porocalices in natural position and can be assumed to be a feature genuine to this particular sponge. Other sections show that strands of ana- or plagiotriaenes (in places reinforced by calthrops) may occur in dense staggered fashion (cladomes facing outward), radiating out in large portions of certain specimens. Crystalline, calcareous spherical bodies of the kind described above, 50–100 μm, are often present in the tissue.

Distribution and ecology.—Material on hand originated from offshore Georgia and South Carolina, 18 to 34 m, and from nearshore to offshore southwest Florida, including Dry Tortugas, 17 to 50 m. Based on dredge hauls, habitats are noted as secondary hard bottoms ("live bottoms"). The type material for this species came from Barbados, off Paynes Bay, 153 m (van Soest & Stentoft 1988). No observations on living sponges are available.

Reexamination of types.—One paratype (ZMA POR. 5267) was reexamined and was found to contain, along with the spicule complement originally described (van Soest & Stentoft 1988:45), a fair number of plagiotriaenes and calthrops. Upon our request, R. W. M. van Soest (Amsterdam) restudied the holotype preparation (ZMA POR. 5266) and confirmed presence of the unusual accessory spicules.

Other material studied.—USNM 33104, off South Carolina, 18 m; USNM 42467, off South Carolina, 34 m; USNM 42468, off Georgia, 28 m; USNM 33217, off southwest Florida, 20 m; USNM 42465 & 42466, off southwest Florida, 17 m; USNM 22442, Dry Tortugas, Florida, 70 m; and 12 uncataloged specimens from the MMS Continental Shelf Survey.

Remarks.—One other recently described species of *Cinachyrella, C. tarentina* (Pulitzer-Finali 1983), shares plagiotriaenes with short rhabds with *C. arenosa.* We studied one specimen of *C. tarentina* obtained from the type locality (courtesy M. Pansini, Genova) but found neither calthrops nor raphids. The habitat of this Mediterranean species is sandy or detrital rock bottom in very shallow (0.5–1 m) water. This distribution, geographical distance, and spicule characteristics prompt us to include our material with *C. arenosa.*

The presence of calthrops in this species would be grounds to place it in *Paratetilla* Dendy, but our analyses of genera and species (Rützler 1987) speak against such classification.

The significance of a second, smaller category of protriaenes and prodiaenes in two of our specimens cannot yet be evaluated. This feature could be a response to unusual or seasonal environmental conditions or a genetic aberration. Only in *C. apion* is it a reliable characteristic although even in this species there are mechanically damaged specimens in which these delicate structures are hardly detectable.

Conclusions

Cinachyrella is a characteristic and easily recognized genus of sponges yet its species are still poorly understood. Our study of large specimen series helped to clarify the taxonomic significance of morphologic characters—spicules in particular—and to define four species that can be recognized in the western Atlantic Ocean. At the same time it was frustrating to find that museum material is of very limited use, despite the fact that it is indispensable as documentation of our findings. The variability of preservable features is enormous and what appears as a clear-cut taxon upon examination of one or a few specimens may, after study of dozens, turn out to be nothing but a section from a spectrum of variants.

It was highly beneficial to our analysis that we were well acquainted with live populations of two of the described species, *Cinachyrella kuekenthali* and *C. apion.* This allowed us to better understand morphological adaptations to changing environmental conditions and effects of different methods of preservation. Reproductive specialization, such as the formation of buds, has significance for the genetic make-up of a population. In our material, this feature was only found in *C. apion* and is still under study, but it has also been reported from at least one Indopacific species, *C. australiensis* (Carter) (Yung-hui Chen, Kaohsiung, Taiwan, pers. comm.). More work on reproduction, ecology, histology, and possibly molecular biology will have to be used to improve the objectivity of taxonomic conclusions.

A particularly curious feature discovered during our study is the apparent formation of presumed calcitic granules inside the tissue of many of these sponges, even enveloping siliceous spicules. The only comparable previous report is by Vacelet et al. (1987) who found similar calcium carbonate spherules in *Hemimycale columella,* representative of a different order (Poecilosclerida) of demosponges. The mechanism and significance of calcium carbonate secretion inside a sponge that also precipitates (simultaneously ?) opaline silica has yet to be determined.

Acknowledgments

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MORPHOLOGY AND TAXONOMY OF TWO NEW SPECIES OF MARINE CILIATES (CILIOPHORA: SPIROTRICHEA: STICHOTRICHIDA: AMPHISIELLIDAE)

Gregorio Fernandez-Leborans and Apolonia Novillo

Abstract.—The morphological characteristics of two ciliate marine protozoan species of subclass Stichotrichia (*Amphisiella ovalis* and *A. arenicola*) are described, with special emphasis on the infraciliature of these organisms. A statistical study has been made of the most important morphological features. The organisms were classified through a comparative analysis with the most similar species.

The "hypotrichs" constitute one of the groups of ciliate protozoa most studied (Corliss 1979). The traditionally well known "hypotrichs" had formed a unique taxonomic group until several years ago: the order Hypotrichida Stein, 1859 (Honigberg et al. 1964, Levine et al. 1980). However, recently, the species of these ciliates have been included in two major groups: subclass Stichotrichia Small & Lynn, 1985 and subclass Hypotrichia Small & Lynn, 1985, that differ mainly regarding to the kinetosomic derivatives of the somatic and oral infraciliature (Lee et al. 1985).

Most ciliate species described, including the "hypotrichs," come from freshwater environments (Kahl 1935; Song & Wilbert 1989; Dragesco & Dragesco-Kérneis 1986; Foissner 1979, 1982, 1988; Blatterer & Foissner 1988). The marine forms are least well known (Dragesco 1960; Agamaliev 1983; Borror 1963, 1965), due on the one hand to fixation and impregnation problems that involve the salt water, and on the other hand to the fact that an important fraction of species pertain to interstitial (psammophilic) fauna and wherein there are difficulties in separating the organisms from the sediment. We have described some marine ciliate species (Fernandez-Leborans 1984a; Fernandez-Leborans & Castro de Zaldumbide 1984, 1985, 1986a, 1986b). Taking into account the modifications of some removal and staining techniques (Fernandez-Leborans & Castro de Zaldumbide 1986a, Fernandez-Leborans 1990), we have studied the morphology of two marine "hypotrichs." The results are shown below.

Methods

The samples were collected in a littoral area of: a) the Mediterranean Sea (Gandía, Spain) (Species I) from a beach zone situated at 38°01′42″N and 0°10′28″E; b) the Cantabric Sea (Castrourdiales, Spain), beside the Atlantic Ocean, a beach zone facing north towards the open sea, at 43°22′N and 0°28′W. The method described by Fernandez-Leborans (1990) was used for ciliates removal, utilizing an initial fixation of 0.3% formaldehyde in sea water. The specimens were treated with the silver carbonate technique (Fernandez-Leborans & Castro de Zaldumbide 1986a) for the observation of infraciliature components and other morphological structures. Photomicrographs and drawings with a camera lucida were obtained from microscopical observation of permanent preparations. The measures were made with an ocular micrometer.

Results

Species I

General morphology.—Organisms elongated ovals, with dorsal and ventral sides flattened. Length of the body varies between

132 μm and 162 μm; width, 37.5 to 67.5 μm. Two oval macronuclei located in middle region of ciliate, each measuring 19.5–31.5 μm long and 9–13.2 μm wide. Beside each macronucleus is an oval micronucleus measuring 6.75–7.5 μm long and 3.15–4.5 μm wide (in some specimens a total of three micronuclei were observed). Ciliature developed most profusely on ventral surface of ciliate, while on dorsal surface there are only 5–6 kineties. Ventral ciliature forms two groups of structures: the oral ciliature and the cirri.

The oral ciliature.—Located on left side of ventral surface. Oral area has a length of 55.5–64.8 μm and a width of 9–21 μm. Its posterior end is 81–99 μm the posterior pole of ciliate, consisting of two structures: the 'adoral organelles zone' (AO) and the 'paroral formation' (PF).

Adoral zone of organelles (AO) is 72–88.5 μm long and situated near left side of ciliate and following the edge of anterior pole of the organism and a part of anterior right side. It comprises 36–42 organelles (polykineties), which are disposed in three zones: a) an 'anterior part' with 15–17 organelles is located on area situated in the anterior left part, the anterior end and a small segment of anterior right edge of ventral surface; organelles of this zone are a length of 2.1–3.15 μm. These structures have three parallel kineties, with 2, 6 and 6 kinetosomes each; b) an 'intermediate part' of 16–19 organelles located on left side of ciliate. Each organelle has a length of 4.5–6.22 μm and is composed of three rows (with 2, 10–14 and 10–14 kinetosomes each); c) a 'posterior part' which is the region nearest to equator of organism. It consists of 5–6 organelles; each organelle 1.2–2.4 μm long and having 2 rows of 6–8 kinetosomes each. On the most posterior segment of this part, the next to last organelle has 2 rows of 4 kinetosomes each, and the last organelle is composed of 2 rows of 2 kinetosomes each.

The 'paroral formation' (PF) delimits the right side of oral area and is formed of two components: 1) 'paroral formation 1' (PF1) nearest to adoral zone of organelles, and 2) 'paroral formation 2' (PF2) located beside the frontal cirri of ciliate. Paroral formation 1 is 25.5–28.8 μm long and has a single row of 60–68 kinetosomes (stichomonad). Paroral formation 2 is 30–35 μm and is formed of 50–52 pairs of kinetosomes (diplostichomonad or diplokinety). In some specimens this structure (PF2) appears divided in two segments: PF2a, anterior, smaller (12–13.8 μm long), and PF2b, posterior (18–21 μm long).

The cirri.—Located on ventral surface of ciliate. There are five groups of cirri: frontal cirri (FC), right marginal cirri (RMC), left marginal cirri (LMC), ventral cirri (VC) and transverse cirri (TC). No caudal cirri are present.

Frontal cirri (FC).—Situated in anterior region of ciliate, between right side and paroral formation. There are four anterior cirri of similar size and three posterior cirri or frontoterminal cirri of lesser size. These last cirri are located near the anterior end of right marginal cirri. Each anterior frontal cirrus is 1.68–2.34 μm and has four rows of 4–6 kinetosomes each. Each frontoterminal cirri is 1.28–1.75 μm long and consists of three rows of 3–4 kinetosomes each.

Right marginal cirri (RMC).—Occupy a zone of 82.5–93 μm long on right side of ventral surface, between anterior region near frontoterminal cirri and posterior part close to transverse cirri of organism. There are 50–54 right marginal cirri, each of them with a length of 2.4–3.2 μm and two rows of 6–8 kinetosomes each. From each cirrus there is a thick derivative running from cirrus to anterior right side of ciliate. This derivative (d1) has a length of 1.6–2.1 μm.

Left marginal cirri (LMC).—Are included in an area 102–118.5 μm long located on left side of ventral surface between anterior zone near adoral organelles and posterior end of ciliate. There are 48–50 cirri of this type, each of them is 2.34–2.64 μm long and one has two rows of 4–6 kinetosomes each.

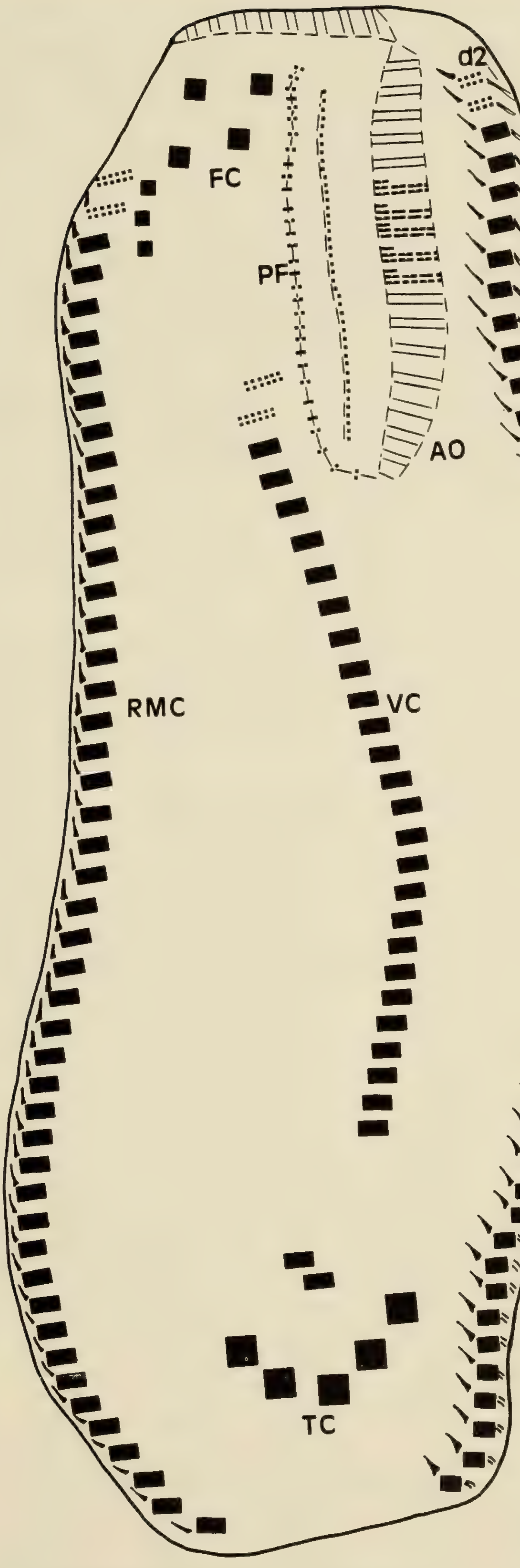

Fig. 1. Infraciliature of *Amphisiella arenicola*. FC, frontal cirri. AO, adoral zone of organelles. RMC, right marginal cirri. LMC, left marginal cirri. VC, ventral cirri. PF, paroral formation. TC, transverse cirri. d1 and d2, kinetosomal derivatives.

Table 1.—Morphometric data on *Amphisiella arenicola*. A, arithmetic mean. B, standard deviation. C, standard error. D, Pearson coefficient. E, coefficient of variation. F, minimum. G, maximum. 1, length of body. 2, width of body. 3, length of each macronucleus. 4, width of each macronucleus. 5, length of the micronucleus. 6, width of the micronucleus. 7, length of the oral area. 8, width of the oral area. 9, length of the right marginal cirri zone. 10, length of the ventral cirri zone. 11, length of the left marginal cirri zone. 12, length of each ventral cirrus. 13, length of each right marginal cirrus. 14, length of each left marginal cirrus. 15, length of each cirrus located directly above the transverse cirri. 16, length of each transverse cirrus. 17, width of each transverse cirrus. 18, length of derivative *1* of the right marginal cirri. 19, length of the derivative *1* of the left marginal cirri. 20, length of derivative *2* of the left marginal cirri. 21, length of the segment *a* of the paroral formation 2 (PF2). 22, length of the segment *b* of the paroral formation 2. 23, length of the paroral formation 1 (PF1). 24, distance between anterior pole and the anterior end of the ventral cirri zone. 25, distance between the anterior pole and the posterior end of the ventral cirri zone. 26, distance between the anterior pole and the anterior end of the transverse cirri zone. 27, distance between the posterior end of the oral area and the posterior pole. 28, length of the adoral zone of organelles (AO). 29, length of each organelle on the anterior part of AO. 30, length of each organelle on intermediate part of AO. 31, length of each organelle on the posterior part of AO. 32, length of each anterior frontal cirrus. 33, width of each anterior frontal cirrus. 34, length of each frontoterminal cirrus. 35, width of each frontoterminal cirrus. 36, distance between the cirri located directly above the transverse cirri and the transverse cirri. 37, distance between the cirri located directly above the transverse cirri and the posterior end of the ventral cirri zone. 38, number of ventral cirri. 39, number of right marginal cirri. 40, number of left marginal cirri. 41, number of transverse cirri. 42, number of adoral organelles. 43, number of kinetosomes of the paroral formation 2 (PF2). 44, number of kinetosomes of the paroral formation 1 (PF1). 45, number of dorsal kineties. (Number of observations: 80.)

	1	2	3	4	5	6	7	8	9
A	144.15	43.53	24.12	11.60	7.06	3.47	60.26	13.64	85.98
B	6.63	7.71	3.11	1.07	0.23	0.38	2.26	2.88	2.67
C	0.74	0.86	0.34	0.12	0.02	0.04	0.25	0.32	0.29
D	0.24	0.13	0.68	0.37	−0.13	−0.33	0.55	0.56	−0.11
E	4.60	17.73	12.90	9.22	3.25	10.95	3.76	21.12	3.10
F	132.00	37.50	19.50	9.00	6.75	3.15	55.50	9.00	82.50
G	162.00	67.50	31.50	13.20	7.50	4.50	64.80	21.00	93.00

	10	11	12	13	14	15	16	17	18
A	81.40	112.78	2.42	2.88	2.45	2.27	2.11	1.44	1.82
B	2.70	3.83	0.44	0.23	0.08	0.08	0.25	0.08	0.11
C	0.30	0.42	0.04	0.02	0.009	0.009	0.02	0.08	0.01
D	0.44	0.07	0.51	0.37	0.44	−0.25	0.07	0.59	0.21
E	3.31	3.40	18.16	7.98	3.27	3.59	11.84	5.55	6.09
F	78.00	102.00	1.80	2.40	2.34	2.10	1.50	1.35	1.62
G	89.00	118.50	3.60	3.25	2.64	2.40	2.45	1.65	2.10

	19	20	21	22	23	24	25	26	27
A	3.92	7.75	13.10	19.33	26.94	29.98	108.81	120.83	85.85
B	0.51	0.69	0.48	0.76	0.81	1.34	3.62	1.23	5.49
C	0.05	0.07	0.05	0.08	0.09	0.15	0.40	0.13	0.61
D	0.23	0.21	0.42	0.43	−0.19	0.73	0.22	0.51	0.33
E	13.01	8.95	3.66	3.97	3.00	4.48	3.32	1.01	6.39
F	2.92	6.60	12.00	18.00	25.50	28.50	100.50	118.00	81.00
G	5.25	9.60	13.80	21.00	28.80	33.00	117.00	123.00	99.00

	28	29	30	31	32	33	34	35	36
A	80.33	2.79	5.64	1.87	1.76	1.47	1.46	1.50	8.47
B	3.77	0.32	0.40	0.39	0.18	0.11	0.16	0.09	0.75
C	0.42	0.03	0.04	0.04	0.02	0.01	0.01	0.01	0.08
D	0.24	−0.62	0.11	−0.36	0.34	0.36	0.74	−0.11	0.09

Table 1.—Continued.

	28	29	30	31	32	33	34	35	36
E	4.69	11.46	7.09	20.85	10.22	7.48	10.95	6.06	8.85
F	72.00	2.10	4.50	1.20	1.68	1.38	1.28	1.31	7.50
G	88.50	3.15	6.22	2.40	2.34	1.80	1.75	1.70	10.50

	37	38	39	40	41	42	43	44	45
A	13.02	53.66	52.16	49.00	5.16	38.33	50.58	63.91	5.66
B	0.57	1.15	1.02	0.73	0.38	1.55	0.79	1.88	0.49
C	0.06	0.12	0.11	0.08	0.04	0.17	0.08	0.21	0.05
D	0.22	−0.28	0.16	0.00	0.42	0.21	0.73	−0.04	−0.67
E	4.42	2.14	1.95	1.48	7.35	4.06	1.56	2.94	8.68
F	12.00	52.00	50.00	48.00	5.00	36.00	50.00	60.00	5.00
G	14.25	56.00	54.00	50.00	6.00	42.00	52.00	68.00	6.00

There is a kinetosomic derivative with an arrangement similar to derivative 'd1' of right marginal cirri, although it is larger (2.92–5.25 μm). Also, each of these cirri has another derivative, like a bundle situated from cirrus to left posterior region of ventral surface. It is 6.6–9.6 μm long.

Ventral cirri (VC).—This group is arranged anteroposteriorly in middle zone of ventral surface, from region close to half of paroral formation 2 (PF2) to posterior region of body. The ventral cirri zone is 78–89 μm long and its anterior end is located 100.5–117 μm from anterior end of ciliate. There are 52–56 ventral cirri, each one with a length of 1.8–3.6 μm and composed of two rows of 6–8 kinetosomes each. Slightly separated from ventral cirri zone there are 2 cirri located directly above the transverse cirri. These cirri are 12–14.2 μm from posterior end of ventral cirri zone and they are 7.5–10.5 μm from the transverse cirri. Each of these cirri has a length of 2.1–2.4 μm and comprises two rows of 5–6 kinetosomes each.

Transverse cirri (TC).—There are 5–6 transverse cirri located near posterior pole of ciliate. These cirri are 118–123 μm from anterior pole of organism. Each cirrus has a length of 1.5–2.4 μm and a width of 1.35–1.65 μm, and consists of four rows of 3–4 kinetosomes each (Fig. 1, Table 1).

Species II

General morphology.—Oval in shape, with posterior end rounded and anterior end slightly pointed. Ciliates 49.5–63 μm long and 27–46.5 μm wide. Oral area occupies a region on left anterior part of ventral surface and has a length of 18–26.2 μm and a width of 10.5–12.7 μm. Scattered in the ciliate are 32–45 macronuclear nodes, each of them 4.2–9 μm long and 2.1–4.4 μm wide. There are 2–4 micronuclei that have a length of 1.56–2.04 μm each.

Most of the ciliature is located on ventral surface. On the dorsal side there are only four kineties. Ventral ciliature arranged in two structures: oral ciliature and cirri (Fig. 2, Table 2).

Oral ciliature.—Is composed of the adoral zone of organelles (AO) and the paroral formation (PF).

The 'adoral zone of organelles' (AO) is located around left anterior edge of ciliate, and surrounding anterior pole of organism. It has a length of 24–31.2 μm and is formed of 16–19 organelles. On middle region of this zone each organelle has four rows of kinetosomes: a short row of 3–4 kinetosomes, an intermediate row of 9–10 kinetosomes and two parallel rows of 15–16 kinetosomes each. The length of these organelles is 7.8–9 μm. In the posterior end

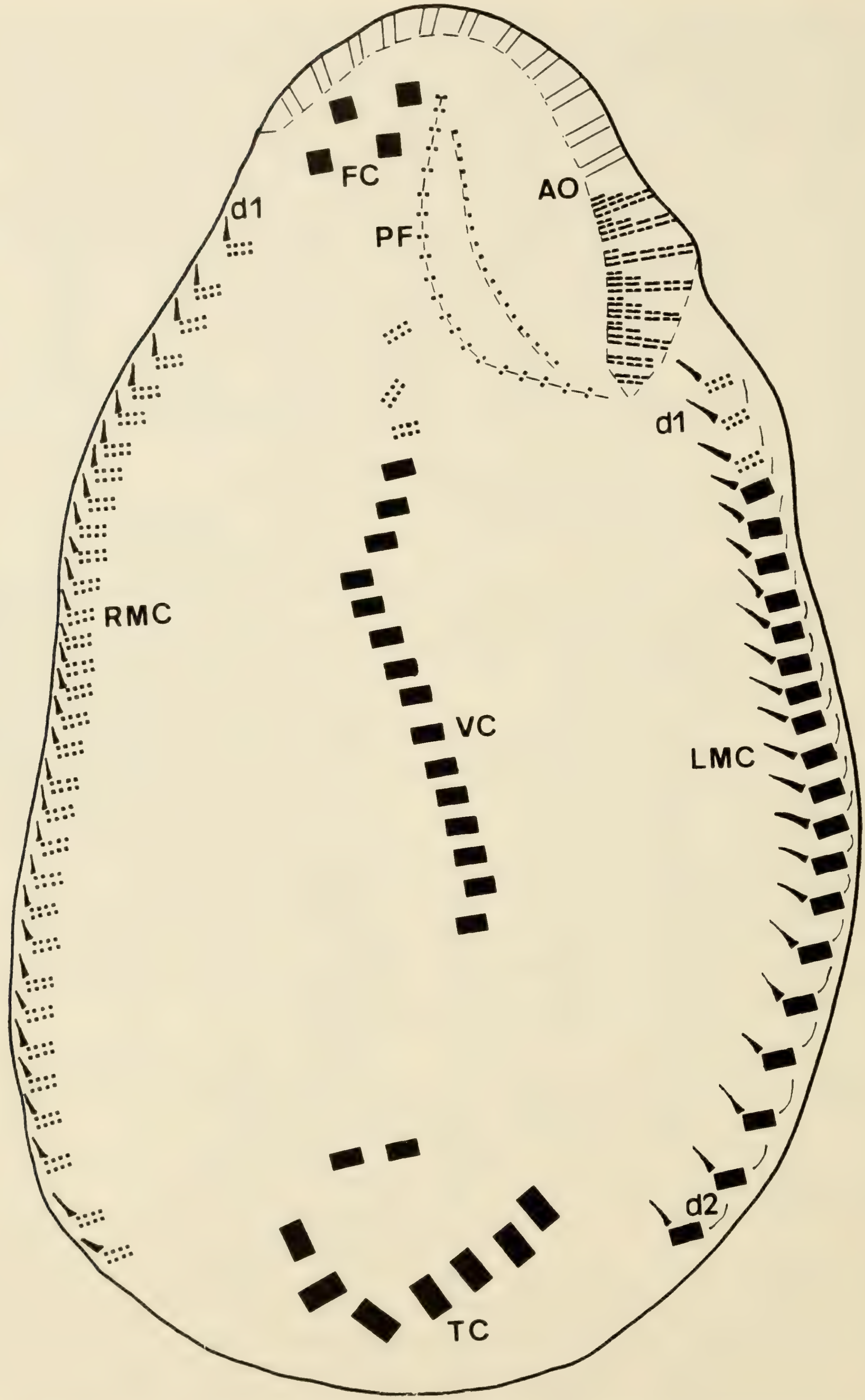

Fig. 2. Infraciliature of *Amphisiella ovalis.* FC, frontal cirri. AO, adoral zone of organelles. PF, paroral formation. RMC, right marginal cirri. LMC, left marginal cirri. VC, ventral cirri. TC, transverse cirri. d1 and d2, kinetosomal derivatives.

Table 2.—Morphometric data on *Amphisiella ovalis*. A, arithmetic mean. B, standard deviation. C, standard error. D, Pearson coefficient. E, coefficient of variation. F, minimum. G, maximum. 1, length of the body. 2, width of the body. 3, length of the oral area. 4, width of the oral area. 5, length of each macronuclear node. 6, width of each macronuclear node. 7, length of each micronucleus. 8, length of the adoral zone of organelles (AO). 9, length of the paroral formation 1 (PF1). 10, length of the paroral formation 2 (PF2). 11, length of each organelle of AO (middle region). 12, length of the left marginal cirri zone. 13, length of the right marginal cirri zone. 14, length of the ventral cirri zone. 15, length of derivative *d1* of the left marginal cirri. 16, length of derivative *d2* of the left marginal cirri. 17, length of derivative *d1* of the right marginal cirri zone. 18, distance between the posterior end of the transverse cirri zone and the anterior pole. 19, distance between the posterior end of the transverse cirri zone and the posterior pole. 20, distance between the posterior end of the ventral cirri zone and the anterior pole. 21, distance between the anterior end of the left marginal cirri zone and the anterior pole. 22, number of adoral organelles. 23, number of kinetosomes of the paroral formation 1 (PF1). 24, number of kinetosomic pairs of the paroral formation 2 (PF2). 25, number of right marginal cirri. 26, number of left marginal cirri. 27, number of ventral cirri. 28, number of macronuclear nodes. 29, number of transverse cirri. 30, number of micronuclei. 31, length of each frontal cirrus. 32, width of each frontal cirrus. 33, length of each right marginal cirrus. 34, length of each left marginal cirrus. 35, length of each ventral cirrus. 36, distance between the transverse cirri zone and the cirri located directly above the transverse cirri. 37, length of each transverse cirrus. 38, width of each transverse cirrus. 39, length of each cirrus located directly above the transverse cirri. (Number of observations: 80.)

	1	2	3	4	5	6	7	8	9	10
A	55.09	31.01	21.58	11.44	5.93	3.80	1.91	29.13	15.44	20.68
B	4.30	5.02	1.95	0.54	1.08	0.56	0.12	2.36	0.65	0.45
C	0.48	0.56	0.21	0.06	0.12	0.06	0.01	0.26	0.07	0.05
D	0.62	0.40	0.50	0.25	0.30	0.00	0.12	−0.45	0.66	0.18
E	7.80	16.18	9.03	4.72	18.21	14.73	6.28	8.10	4.20	2.17
F	49.50	27.00	18.00	10.50	4.20	2.10	1.56	24.00	14.40	19.80
G	63.00	46.50	26.20	12.70	9.00	4.40	2.04	31.20	16.80	21.60

	11	12	13	14	15	16	17	18	19	20
A	8.29	41.12	54.00	28.90	3.79	2.23	2.85	48.51	8.11	46.78
B	0.34	2.80	1.90	1.30	0.44	0.17	0.24	1.76	0.90	0.83
C	0.03	0.31	0.21	0.14	0.04	0.01	0.02	0.19	0.10	0.09
D	0.01	−0.34	0.31	0.23	−0.003	0.20	−0.59	0.29	1.01	0.45
E	4.10	6.80	3.51	4.49	11.60	7.62	8.42	3.62	11.09	1.77
F	7.80	36.30	50.10	26.50	2.46	1.86	2.40	45.00	6.60	45.00
G	9.00	45.00	58.50	31.60	4.20	2.52	3.18	52.50	9.60	48.20

	21	22	23	24	25	26	27	28	29	30
A	23.19	17.50	23.25	25.33	31.33	22.41	19.66	40.25	6.75	2.50
B	0.52	0.90	1.05	0.88	0.88	1.08	1.07	3.69	0.45	0.79
C	0.05	0.10	0.11	0.09	0.09	0.12	0.11	0.41	0.05	0.08
D	0.17	−0.55	0.23	−0.75	−0.75	0.38	−0.31	−0.47	−0.55	0.62
E	2.24	5.14	4.51	3.47	2.80	4.81	5.44	9.16	6.70	31.90
F	22.80	16.00	22.00	24.00	30.00	20.00	18.00	32.00	6.00	2.00
G	24.60	19.00	25.00	26.00	32.00	24.00	22.00	45.00	7.00	4.00

	31	32	33	34	35	36	37	38	39
A	2.32	1.45	1.74	1.69	1.75	5.52	1.76	1.05	1.58
B	0.08	0.08	0.07	0.04	0.06	0.29	0.06	0.07	0.06
C	0.009	0.009	0.008	0.004	0.007	0.03	0.006	0.008	0.007
D	0.24	0.61	0.45	0.41	0.48	0.40	0.48	−0.57	0.31
E	3.81	6.10	4.47	2.50	3.69	5.42	3.42	7.44	4.32
F	2.10	1.38	1.56	1.62	1.69	4.80	1.62	0.96	1.44
G	2.46	1.68	1.86	1.80	1.92	6.00	1.86	1.20	1.74

Table 3.—Comparison among the most similar species. a, *Amphisiella terricola* (Hemberger, 1982). b, *Holostichides terricola*. c, *Amphisiella australis* (Population I). d, *Amphisiella australis* (Population II). e, *Amphisiella magnigranulosa*. f, *Trachelochaeta gonostomoida*. g, *Uroleptoides atypica*. h, *Uroleptoides binucleata*. i, *Uroleptoides caudata*. j, *Amphisiella capitata*. k, *Amphisiella acuta*. l, *Perisincirra gellerti* (Population I). m, *Perisincirra gellerti* (Population II). n, *Amphisiella terricola*. o, *Amphisiella oscensis*. p, *Amphisiella milnei*. q, *Amphisiella arenicola* (Species I). r, *Amphisiella ovalis* (Species II). 1, length of the body. 2, width of the body. 3, length of the adoral zone of organelles. 4, length of each macronucleus. 5, width of each macronucleus. 6, length of the

	1	2	3	4	5	6	7	8
a	190–230	85–100	41 (d)	23.3–25 (d)	14–15 (d)	6.6 (d)	2	2
b	72–115	14–19	18–23	3–10	2–5	2–3	14–18	2–5
c	98–145	32–48	22–29	17–22	9–11	3–4	2	2–5
d	87–122	24–49	16–25	11–20	7–9	3–4	2	1–4
e	84–123	40–56	21–28	15–24	6–10	3–4	2	2–6
f	110–200	30–50	37 (d)	15–16 (d)	8–10 (d)	3.8 (d)	2	2
g	200	30–40	30 (d)	3.7–7.5 (d)	2.5–4 (d)	3–5 (d)	23	2
h	220–260	50	35 (d)	30 (d)	11–13 (d)	5.8 (d)	2	2
i	200	50	22 (d)	5–6.8 (d)	3–4.3 (d)	2.5 (d)	14	4–6
j	65 (d)	18 (d)	46 (d)	—	—	—	—	—
k	86–147	14–17	13–16	4–6.4	1.4–2.6	1.5 (d)	24–38	2
l	50–79	11–15	14–18	2.6–8	1.5–5.3	1.3 (d)	6–13	2
m	48–65	9–14	13–21	4–8	2–4	1.3 (d)	6–8	2
n	86–108	38–55	27–28	11–15	10–11	2.3 (d)	2	2
o	77–81	31–33	30.4	17	9.1	1.36	2	2
p	120	35	65 (d)	20–24 (d)	8–11 (d)	2 (d)	2	2–3
q	132–162	37.5–67.5	72–88	19.5–31.5	9–13.2	6.7–7.5	2	2–3
r	49–63	27–46	24–31.2	4.2–9	2.1–4.4	1.5–2.04	32–45	2–4

of the adoral zone the last organelle has two rows of 6–8 kinetosomes each.

The 'paroral formation' (PF) delimits the right side of the buccal cavity. It consists of two structures: a) an internal part (PF1), which is shorter, has a single row (stichomonad) of 22–25 kinetosomes, and is 14.4–16.8 μm long; b) an external part (PF2), which is longer than PF1 and reaches the posterior end of the adoral zone. It is 19.8–21.6 μm long and comprises 24–26 pairs of kinetosomes (diplostichomonad).

The cirri.—There are five types of cirri: frontal (FC), right marginal (RMC), left marginal (LMC), ventral (VC) and transverse (TC). No caudal cirri are present.

Frontal cirri (FC).—Located in anterior area of ventral surface, between paroral formation and right side. There are four frontal cirri, each of them having a length of 2.1–2.46 μm and a width of 1.38–1.68 μm. Each cirrus consists of four rows of kinetosomes of which number varies on different cirri. On frontal cirrus F1 (the most anterior and close to paroral formation) there is a row of 3–4 kinetosomes and three rows of 4 kinetosomes each. On F2 cirrus (anterior and close to right side of ventral surface) there is a row of 4–6 kinetosomes and three rows of 6 kinetosomes each. On F3 cirrus (posterior and near to paroral formation) there are four rows of 6 kinetosomes each. On F4 cirrus (posterior and close to right side of ventral surface) there are two rows of 6 kinetosomes each and two rows of 6–8 kinetosomes each.

Right marginal cirri (RMC).—They occupy a great part of right border on ventral surface of ciliate. The zone of these cirri has a length of 50.1–58.5 μm; its anterior end is located near anterior end of adoral zone of organelles that overhang in right side and its posterior end is situated near to posterior pole of ciliate. There are 30–32 right mar-

Table 3.—Extended.
micronucleus. 7, number of macronuclei. 8, number of micronuclei. 9, number of dorsal kineties. 10, number of adoral organelles. 11, number of right marginal cirri. 12, number of left marginal cirri. 13, number of frontal cirri. 14, number of ventral cirri. 15, number of transverse cirri. 16, number of caudal cirri. 17, structure of the paroral formation (d: diplostichomonad; st: stichomonad; sd: stichodyad; p: polystichomonad). 18, distance between the anterior pole and the posterior end of the ventral cirri zone. 19, number of buccal cirri. (d, data from the author's drawings.)

9	10	11	12	13	14	15	16	17	18	19
3	26–28	40–45	35–40	8–10	26–30	6–8	0	d	80 (d)	—
2	17–21	22–31	20–35	6–7	11–17	0	3	st + st	45 (d)	0
3	22–27	41–56	37–53	5–9	12–23	4–6	0	st + st	45–73	1
3–4	20–24	33–49	35–52	5–9	15–21	5–6	0	st + st	40–66	1
2–3	21–25	35–54	38–60	6–8	12–19	3–6	0	st + st	28–63	1
3	33	18–27	12–15	9	17–18	2	3	st + st	74 (d)	1
4	23–25	47–55	47–53	6	27–30	3	3	d	55 (d)	1
3	24–28	60	55	6	33–40	3	0	d + d	85 (d)	1
3	35	37–39	24–35	4	38	0	0	d	72 (d)	1
—	—	20	22	10	22	5	0	st	58 (d)	1
3	13–16	35–54	36–55	4	15–24	3	0	sd + sd	39–57	1
4	13–17	14–20	15–20	4	6–14	2–5	0	sd + st	23–21	1
4–5	13–17	13–19	11–19	4	8–12	3–5	0	sd + st	12–29	1
3	27–31	47–56	35–43	8	30–35	6–7	0	sd + sd	63–70	1
3	38–41	32–34	28–30	4	17–28	5	6–7	(d + st) + (st + p)	52–56	1
—	30–35	36–44	36–44	6–9	36–44	5	0	st	100 (d)	—
5–6	36–42	50–54	48–50	7	52–56	5–6	0	st + d	100.5–117	—
4	16–19	30–32	20–24	4	18–22	6–7	0	st + d	45–48.2	—

ginal cirri, each of them (1.56–1.86 μm long) having two rows of 4 kinetosomes each. These cirri dispose of a thick derivative (d1) arranged from cirrus to anterior right zone of ciliate; it is 2.4–3.18 μm long.

Left marginal cirri (LMC).—Located between posterior end of adoral zone of organelles and posterior pole, on left side of ventral surface. The zone of left marginal cirri has a length of 36.3–45 μm and its anterior end is 22.8–24.6 μm from anterior end of ciliate. This zone consists of 20–24 cirri, each one formed of two rows of 4 kinetosomes each. The 4–6 most posterior cirri have an additional row of 4 kinetosomes. Every cirrus (1.62–1.8 μm long) has two types of derivatives: d1) similar in disposition to derivate 'd1' of right marginal cirri and 2.46–4.2 μm long; and d2) a structure less thick than 'd1' and located from cirrus to left anterior area of organism with a length of 1.86–2.52 μm.

Ventral cirri (VC).—Constitute a group more or less sinuous, 26.5–31.6 μm long, situated in middle region of ventral surface, with anterior end near to paroral formation 2 (PF2). There are 18–22 ventral cirri, each one 1.69–1.92 μm long and formed of two rows: the anterior possesses 4–5 kinetosomes and the posterior one has 4–6 kinetosomes.

Directly above the transverse cirri and separated from the ventral cirri set, are two cirri of similar structure to the ventral cirri. These cirri are located 4.8–6 μm from transverse cirri set and are 1.44–1.74 μm long. They have two rows of 4–6 kinetosomes each.

Transverse cirri (TC).—There are six or seven transverse cirri located near posterior pole of organism. They are 45–52.5 μm from anterior end and 6.6–9.6 μm from posterior end of ciliate. Each cirrus is 1.62–1.86 μm long and 0.96–1.2 μm wide. Kinetosomic

Table 4.—Comparison of the arithmetic means (*t*) and variances (*f*) between *Amphisiella arenicola* (Species I) and the similar species (+, significant difference; −, non-significant difference; ( ) 99% signification; = data not available). a, *Holostichides terricola.* b, *Amphisiella australis* (Population I). c, *Amphisiella australis* (Population II). d, *Amphisiella magnigranulosa.* e, *Amphisiella acuta.* f, *Perisincirra gellerti* (Population I). g, *Perisincirra gellerti* (Population II). h, *Amphisiella terricola* (Foissner, 1984). i, *Amphisiella ovalis* (Species II). 1, length of the body. 2, width of the body. 3, length of the adoral zone of organelles. 4, length of each macronucleus. 5, width of each macronucleus. 6, length of the micronucleus. 7, number of macronuclei. 8, number of micronuclei. 9, number of dorsal kineties. 10, number of adoral organelles. 11, number of right marginal cirri. 12, number of left marginal cirri. 13, number of ventral cirri. 14, number of transverse cirri. 15, distance between the anterior pole and the posterior end of the ventral cirri zone.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	*t*	18.01	3.65	124.43	34.84	49.41	61.02	44.19	4.16	73.2	62.67	37.86	24.11	=	=	=
	Sig.	+	+	+	+	+	+	+	+	+	+	+	+	=	=	=
	f	3.10	15.59	11.19	4.07	3.05	1.8	0	0	0	1.89	8.38	33.20	=	=	=
	Sig.	+	+	+	+	+	+ (−)	−	−	−	−	+	+	=	=	=
b	*t*	5.96	1.83	69.52	6.12	7.27	42.88	0	4.28	53.2	31.84	0.10	1.27	33.32	0.23	17.59
	Sig.	+	−	+	+	+	+	−	+	+	+	−	−	+	−	+
	f	4.79	2.3	2.5	2.49	2.18	1.8	0	0	0	1	21.57	48.5	10.54	2.6	7.72
	Sig.	+	−	−	−	−	−	−	−	−	−	+	+	+	+	+
c	*t*	11.38	5.22	75.67	9.02	20	67.66	0	3.33	=	37.81	8.24	45.1	59.6	3.14	23.32
	Sig.	+	+	+	+	+	+	−	+	=	+	+	+	+	+	+
	f	3.73	1.16	2.31	1	2.18	1.25	0	0	=	1	23.32	54.24	3.91	1.8	5.88
	Sig.	+	+	+ (−)	−	−	−	−	−	=	−	+	+	+	+ (−)	+
d	*t*	12.86	1.86	83.72	5.54	14	44	0	4.19	19.06	41.13	7.75	2.04	64.75	1.18	21.71
	Sig.	+	+	+	+	+	+	−	+	+	+	+	+ (−)	+	−	+
	f	2.69	2.3	3.67	1.14	1.06	1.8	0	0	1.12	1.56	25.48	101.83	3.25	4.6	7.25
	Sig.	+ (−)	−	+ (−)	−	−	−	−	−	−	−	+	+	+	+	+
e	*t*	6.38	32.19	139.63	46.63	74.61	=	24.54	=	53.2	90.88	3.81	2.68	48.41	50.23	38.68
	Sig.	+	+	+	+	+	=	+	=	+	+	+	+	+	+	+
	f	7.57	87.42	16.4	14.18	12.88	=	0	0	0	4.62	33.12	65.62	5.08	0	2.57
	Sig.	+	+	+	+	+	=	−	−	−	+	+	+	+	−	+
f	*t*	30.58	32.9	122.5	30.2	22.77	=	10.3	=	33.2	54.25	63.61	73.63	65.01	6.64	102.01
	Sig.	+	+	+	+	+	=	+	=	+	+	+	+	+	+	+
	f	1.59	32.25	10.77	3.44	1.15	=	0	0	0	1.29	3.36	4.01	3.65	8.93	2.47
	Sig.	−	+	+	+ (−)	−	=	−	−	−	−	+	+	+	+	−

Table 4.—Continued.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
g	*t*	49.91	33.43	92.32	39	52.35	=	33.52	=	7.81	23.2	73.92	53.65	132.6	9	67.48
	Sig.	+	+	+	+	+	=	+	=	+	+	+	+	+	+	+
	f	1.3	28.31	3.31	6.23	4.29	=	0	0	1.41	2.24	2.94	9.77	1.01	1.8	1.44
	Sig.	−	+	+ (−)	+	+	=	−	−	−	−	+	+	−	−	−
h	*t*	12.75	0.04	112.6	11.54	3.66	=	0	=	=	12.75	1.15	7.62	18.56	=	=
	Sig.	+	−	+	+	+	=	−	=	=	+	−	+	+	=	=
	f	2.22	1.07	39.02	2.45	2.63	=	0	0	=	1.17	22.71	22.64	5.52	=	=
	Sig.	−	−	+	−	−	=	−	−	=	−	+	+	+	=	=
i	*t*	101.2	12.27	108.93	50.52	70.9	257.5	93.29	6.25	33.2	104.15	148.78	132.95	266.66	26.5	151.29
	Sig.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	f	2.38	2.35	2.56	8.22	3.62	5	0	0	0	2.98	1.37	2.18	1.15	1.33	19.26
	Sig.	+	+	+	+	+	+	−	−	−	+	−	+	−	−	+

composition varies among cirri. Numbered from left to right, the number of kinetosomes of each row is the following:

T1 = 3–4 + 4 + 3–4
T2 = 3 + 3–4 + 4
T3 = 4 + 4 + 3–4
T4 = 4–6 + 4–6 + 4–5
T5 = 3 + 3–4 + 3
T6 = 4 + 4 + 3–4
T7 = 3–4 + 4–6 + 4–6

Taxonomic Position

The two species studied belong to subkingdom Protozoa Goldfuss, 1818, emd. Von Siebold, 1846; phylum Ciliophora Doflein, 1901; subphylum Postciliodesmatophora Gerassimova & Seravin, 1976; class Spirotrichea Bütschli, 1889; subclass Stichotrichia Small & Lynn, 1985 and order Stichotrichida Fauré-Fremiet, 1961 (Lee et al. 1985, Corliss 1979). The species most similar (infraciliature and nuclear structures principally) to these ciliates are: a) *Amphisiella terricola* Gellért, 1955 (Hemberger 1982); b) *Holostichides terricola* Foissner, 1988; c) *Amphisiella australis* Blatterer & Foissner, 1988 (Population I); d) *Amphisiella australis* Blatterer & Foissner, 1988 (Population II); e) *Amphisiella magnigranulosa* Foissner, 1988; f) *Trachelochaeta gonostomoida* Hemberger, 1985; g) *Uroleptoides atypica* Hemberger, 1985; h) *Uroleptoides binucleata* Hemberger, 1985; i) *Uroleptoides caudata* Hemberger, 1985; j) *Amphisiella capitata* Perejaslawzewa, 1886; k) *Amphisiella acuta* Foissner, 1982; l) *Perisincirra gellerti* Foissner, 1982 (Population I); m) *Perisincirra gellerti* Foissner, 1982 (Population II); n) *Amphisiella terricola* Gellért, 1955 (Foissner 1984); o) *Amphisiella oscensis* Fernandez-Leborans, 1984; and p) *Amphisiella milnei* Kahl, 1932 (Agamaliev 1983; Foissner 1982, 1984, 1988; Blatterer & Foissner 1988; Hemberger 1985; Borror 1972; Fernandez-Leborans 1984b).

The organisms described have been compared with these similar species, taking into

Table 5.—Comparison of the arithmetic means (*t*) and variances (*f*) between *Amphisiella ovalis* (Species II) and the similar species (+, significant difference; −, non-significant difference; ( ) 99% significance; = data not available). a, *Holostichides terricola.* b, *Amphisiella australis* (Population I). c, *Amphisiella australis* (Population II). d, *Amphisiella magnigranulosa.* e, *Amphisiella acuta.* f, *Perisincirra gellerti* (Population I). g, *Perisincirra gellerti* (Population II). h, *Amphisiella terricola* (Foissner, 1984). 1, length of the body. 2, width of the body. 3, length of the adoral zone of organelles. 4, length of each macronucleus. 5, width of each macronucleus. 6, length of the micronucleus. 7, number of macronuclei. 8, number of micronuclei. 9, number of dorsal kineties. 10, number of adoral organelles. 11, number of right marginal cirri. 12, number of left marginal cirri. 13, number of ventral cirri. 14, number of transverse cirri. 15, distance between the anterior pole and the posterior end of the ventral cirri zone.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
a	*t*	12.25	1.99	23.69	1.97	4	5.57	48.13	1.92	9.09	5	8.93	1.93	=	=	=
	Sig.	+	−	+	−	+	+	+	−	+	+	+	−	=	=	=
	f	7.40	37.23	4.37	2.01	1.18	9	7.67	1.68	0	1.57	11.5	15.19	=	=	=
	Sig.	+	+	+	+ (−)	−	+	+	−	−	−	+	+	=	=	=
b	*t*	15.91	6.28	4.32	25.48	31	16.12	93.29	2.41	0	15.11	15.76	17.47	0.63	8.61	4.43
	Sig.	+	+	+	+	+	+	+	+ (−)	−	+	+	+	−	+	+
	f	11.42	1.02	0.97	3.30	1.65	9	0	1.73	0	2.98	29.58	22.19	12.18	1.95	148.75
	Sig.	+	−	−	+	−	+	−	−	−	+	+	+	+	+ (−)	+
c	*t*	14.15	7.83	11.18	12.13	21.11	21.8	93.29	1.15	=	10.23	7.42	13.95	3.86	11.36	2.77
	Sig.	+	+	+	+	+	+	+	−	=	+	+	+	+	+	+
	f	8.89	2.01	1.10	8.19	1.65	4	0	1.38	=	2.96	32	24.82	4.51	1.35	113.43
	Sig.	+	+ (−)	−	+	−	+	−	−	=	+	+	+	+	−	+
d	*t*	16.04	10.32	9.55	16.5	12.85	14.87	93.29	2.5	8.57	14.44	6.71	10.92	6.13	8.40	0.92
	Sig.	+	+	+	+	+	+	+	+ (−)	+	+	+	+	+	+	−
	f	6.42	1.02	1.43	7.18	3.40	9	0	2.09	0	1.91	34.96	46.60	3.75	3.45	139.69
	Sig.	+	−	−	+	+	+	−	+ (−)	−	+ (−)	+	+	+	+	+
e	*t*	11.04	26.35	42.44	3.72	19	=	6.67	=	0	12.72	8.88	13.53	1.17	75	1.35
	Sig.	+	+	+	+	+	=	+	=	−	+	+	+	−	+	−
	f	18.05	37.05	6.40	1.72	3.55	=	1.39	=	0	1.54	45.43	30.03	5.87	0	49.57
	Sig.	+	+	+	−	+	=	−	=	−	−	+	+	+	−	+
f	*t*	3.35	27.07	32.69	0.13	1.14	=	40.32	=	0	6.09	27.07	12.91	14.26	11	28.37
	Sig.	+	+	+	−	−	=	+	=	−	+	+	+	+	+	+
	f	3.79	13.67	4.20	2.38	4.18	=	2.82	=	0	2.30	4.61	1.83	4.22	6.7	7.78
	Sig.	+	+	+	+	+	=	+ (−)	=	−	+ (−)	+	+ (−)	+	+	+

Table 5.—Continued.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
g	*t*	0.42	27.80	21.66	1.47	7.33	=	73.97	=	8	9	32.91	11.26	29.57	19	19.57
	Sig.	−	+	+	−	+	=	+	=	+	+	+	+	+	+	+
	f	1.82	12	1.29	1.31	1.18	=	35.43	=	0	1.32	4.03	4.47	1.13	1.35	27.88
	Sig.	+ (−)	+	−	−	−	=	+	=	−	−	+	+	−	−	+
h	*t*	9.37	4.07	5.08	8.8	23.92	=	93.29	=	=	17.5	8.62	11.42	10.24	=	=
	Sig.	+	+	+	+	+	=	+	=	=	+	+	+	+	=	=
	f	5.28	2.18	15.24	3.34	1.37	=	0	=	=	3.51	31.15	10.36	6.38	=	=
	Sig.	+	−	+	+	−	=	−	=	=	+	+	+	+	=	=

account 19 characteristics: 1) length of the body; 2) width of the body; 3) length of the adoral zone of organelles; 4) length of each macronucleus; 5) width of each macronucleus; 6) length of the micronucleus; 7) number of macronuclei; 8) number of micronuclei; 9) number of dorsal kineties; 10) number of adoral organelles; 11) number of right marginal cirri; 12) number of left marginal cirri; 13) number of frontal cirri; 14) number of ventral cirri; 15) number of transverse cirri; 16) number of caudal cirri; 17) structure of the paroral formation (d: diplostichomonad; st: stichomonad; sd: stichodyad; p: polystichomonad); 18) distance between the anterior pole and the posterior end of the ventral cirri zone; and 19) number of buccal cirri. The number of differences, in relation to these characteristics, between 'Species I' and the other species are: 13 with respect to *Amphisiella terricola* (Hemberger 1982) (a); 16 (b); 8 (c); 10 (d); 10 (e); 14 (f); 16 (g); 13 (h); 16 (i); 10 (j); 14 (k); 15 (l); 13 (m); 13 (n); 14 (o); and 9 with respect to species (p). The number of differences in relation to 'Species II' are: 15 (a); 10 (b); 12 (c); 11 (d); 12 (e); 16 (f); 13 (g); 16 (h); 14 (i); 8 (j); 10 (k); 10 (l); 11 (m); 13 (n); 12 (0) and 13 with respect to species (p). There are 14 differences between the two species studied (Table 3).

On the other hand, a comparative analysis has been made of the arithmetic means and variances. The species with statistical indexes described in the literature have been considered. These species are: a) *Holostichides terricola*; b) *Amphisiella australis* (Population I); c) *Amphisiella australis* (Population II); d) *Amphisiella magnigranulosa*; e) *Amphisiella acuta*; f) *Perisincirra gellerti* (Population I); g) *Perisincirra gellerti* (Population II); h) *Amphisiella terricola* (Foissner 1984). For this analysis the following characteristics have been compared: 1) length of the body; 2) width of the body; 3) length of the adoral zone of organelles; 4) length of each macronucleus; 5) width of each macronucleus; 6) length of the micronucleus; 7) number of macronuclei; 8) number of micronuclei; 9) number of dorsal kineties; 10) number of adoral organelles; 11) number of right marginal cirri; 12) number of left marginal cirri; 13) number of ventral cirri; 14) number of transverse cirri; and 15) distance between the anterior pole and the posterior end of the ventral cirri zone.

In the comparison of arithmetic means, 'Species I' has the lesser number of significant differences (7) with respect to *Amphisiella terricola,* followed by *Amphisiella australis* (Population I) (10), whereas in the comparison of variances the lesser number of significant differences (4) corresponds to *Amphisiella terricola,* followed by *Perisincirra gellerti* (Population II) (6, significance level 95%; 5, significance level 99%) (Table 4).

'Species II' has, on the comparison of arithmetic means, the lesser number of significant differences (8) with respect to *Holostichides terricola,* followed by *Amphisiella acuta* (10), *Perisincirra gellerti* (Population I) (10) and *Amphisiella terricola* (10). In the comparison of variances the lesser number of significant differences refer to *Perisincirra gellerti* (Population II) (6, significance level 95%; 5, significance level 99%), followed by *Amphisiella terricola.* The comparison of arithmetic means between the two species studied shows 15 significant differences (Table 5).

Taking into account this data, we believe that both species belong to the genus *Amphisiella,* and there are sufficient differences with respect to the morphologic features to indicate that they are two new species: *Amphisiella arenicola,* n. sp. ('Species I') and *Amphisiella ovalis,* n. sp. ('Species II'). Type specimens: permanent slides staining with silver carbonate technique, deposited in the Laboratorio de Biología General, Facultad de Biología, Universidad Complutense de Madrid, ref. n. 1663a–f (*Amphisiella arenicola*), ref. n. 1665a–l (*Amphisiella ovalis*)

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 30 September 1991 in Vol. 48, Part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2710 CLAVIDAE McCrady, 1859 (Cnidaria, Hydrozoa) and CLAVINAE Casey, 1904 (Mollusca, Gastropoda): proposal to remove the homonymy.
2766 *Conus fulmen* Reeve, 1843 (Mollusca, Gastropoda): proposed conservation, and *Conus berghausi* Michelotti, 1847: proposed precedence over *C. demissus* Philippi, 1836.
2805 *Ptychagnostus* Jaekel, 1909 and *Glyptagnostus* Whitehouse, 1936 (Trilobita): proposed conservation of accepted usage.
2778 *Asaphus eichwaldi* Fischer von Waldheim in Eichwald, 1825 (currently *Paladin eichwaldi*; Trilobita): proposed conservation of neotype designation.
2671 J. C. Megerle's (1801–1805) auction catalogues of insects: proposed suppression, with conservation of the specific names of *Saperda alboguttata* Megerle, 1803 (now in *Apomecyna*) (Coleoptera) and *Hippobosca variegata* Megerle, 1803 (Diptera).
2751 *Paolia vetusta* Smith, 1871 (Insecta, Protorthoptera): proposed replacement of neotype by rediscovered holotype.
2755 *Eurymeloides* Ashmead, 1889 (Insecta, Homoptera): proposed confirmation of *Eurymela bicincta* Erichson, 1842 as the type species, and designation of a neotype for *E. bicincta.*
2754 *Scoparipes* Signoret, 1880 (Insecta, Heteroptera): proposed confirmation of *Cydnus latipes* Westwood, 1837 as the type species.
2756 *Proagoderus* Lansberge, 1883 (Insecta, Coleoptera): proposed conservation.
1707 *Diabrotica undecimpunctata* Mannerheim, 1843 (Insecta, Coleoptera): proposed conservation of the specific name, and of the subspecific name *howardi* Barber, 1947.
2767 *Drosophila hydei* Sturtevant, 1921 (Insecta, Diptera): proposed conservation of the specific name.
2761 *Chrysops atlanticus* Pechuman, 1949 (Insecta, Diptera): proposed conservation of the specific name.
2535 Proposed precedence of some bee family-group names (Insecta, Hymenop-

tera): names based on *Colletes* Latreille, 1802, on *Paracolletes* Smith, 1853, on *Halictus* Latreille, 1804, on *Anthidium* Fabricius, 1804 and on *Anthophora* Latreille, 1803 to have precedence over some senior names.

2697 *Streptograptus* Yin, 1937 (Graptolithina): proposed designation of *Graptolithus plumosus* Baily, 1871 as the type species.

2771 *Amphiuma tridactylum* Cuvier, 1827 (Amphibia, Caudata): proposed conservation of the specific name.

2778 *Ichthyosaurus trigonus* Owen, 1840 (currently *Macropterygius trigonus*; Reptilia, Ichthyopterygia): proposed replacement of neotype by rediscovered holotype.

The following Opinions were published on 30 September 1991 in Vol. 48, Part 3 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1649 *Pleuractis* Verrill, 1864 (Cnidaria, Anthozoa): *Fungia paumotensis* Stutchbury, 1833 designated as the type species.

1650 CYMATIINAE Iredale, 1913 (1854) (Mollusca, Gastropoda) and CYMATIINAE Walton in Hutchinson, 1940 (Insecta, Heteroptera): homonymy removed.

1651 *Mytilus anatinus* Linnaeus, 1753 (currently *Anodonta anatina*; Mollusca, Bivalvia): neotype designation confirmed.

1652 *Griffithides* Portlock, 1843 (Trilobita): *Griffithides longiceps* Portlock, 1843 confirmed as the type species, and *Bollandia* Reed, 1943 (Trilobita): conserved.

1653 *Mirochernes* Beier, 1930 (Arachnida, Pseudoscorpionida): *Chelanops dentatus* Banks, 1895 confirmed as the type species.

1654 *Fonscolombia* Lichtenstein, 1877 (Insecta, Homoptera): *Fonscolombia graminis* Lichtenstein, 1877 fixed as the type species.

1655 *Curculio viridicollis* Fabricius, 1792 (currently *Phyllobius viridicollis*; Insecta, Coleoptera): specific name conserved, and *Rhyncolus* Germar, 1817: *Curculio ater* Linnaeus, 1758 designated as the type species.

1656 *Longitarsus symphyti* Heikertinger, 1912 (Insecta, Coleoptera): specific name conserved.

1657 *Colias alfacariensis* Ribbe, 1905, *Colias australis* Verity, 1911 and *Colias calida* Verity, 1916 (Insecta, Lepidoptera): availability of specific names confirmed.

1658 *Callionymus pusillus* Delaroche, 1809 (Osteichthyes, Perciformes): specific name conserved.

1659 *Trionyx sinensis* Wiegmann, 1834 (Reptilia, Testudines): specific name conserved.

1660 *Steno attenuatus* Gray, 1846 (currently *Stenella attenuata*; Mammalia, Cetacea): specific name conserved.

1661 *Mammuthus* Brookes, 1828 (Mammalia, Proboscidea): conserved, and *Elephas primigenius* Blumenbach, 1799 designated as the type species.

REVIEWERS

The following people reviewed manuscripts for the *Proceedings* in 1991. D. L. Adkison, C. A. Ahern, F. Alvarez, W. D. Anderson, Jr., M. Bacescu, R. C. Banks, I. Beveridge, D. Billett, J. A. Blake, J. Bocquet-Vedrine, K. J. Boss, T. E. Bowman, G. Boxshall, H. P. Brown, M. R. Browning, N. L. Bruce, R. C. Brusca, J. N. Caira, S. D. Cairns, M. D. Carleton, F. A. Chace, Jr., J. B. Chapin, P. J. Clausen, R. Cocroft, B. B. Collette, J. S. M. Collins, B. C. Coull, R. F. Cressey, A. Crosnier, M. Crump, P. J. F. Davie, G. M. Davis, M. Dojiri, P. L. Dudley, W. E. Duellman, H. J. Dumont, U. Einsle, B. Eliahu, R. Farris, K. Fauchald, D. L. Felder, R. M. Feldman, F. D. Ferrari, F. Fiers, K. Fitzhugh, J. A. Fournier, V. A. Funk, S. Gamo, A. L. Gardner, J. S. Garth, C. J. Glasby, R. B. Griffis, H. Griffith, J. Haig, R. Hanley, S. C. Harris, R. W. Heard, P. C. Heemstra, T. J. Henry, D. A. Hensley, W. R. Heyer, R. P. Higgins, B. Hill, S. Hiruta, J.-s. Ho, H. H. Hobbs, Jr., H. H. Hobbs, III, J. T. Hoeg, K. Hulsemann, R. W. Ingle, C. G. Jara, G. D. Johnson, D. A. Jones, N. S. Jones, Z. Kabata, Q. B. Kamzi, B. Kensley, T. Kikuchi, Y. Kikuchi, C. von V. Klein, D. Kritsky, P. Lambert, R. Lemaitre, D. Lipscomb, J. D. Lynch, E. Macpherson, R. B. Manning, J. C. Markham, E. L. Markhaseva, J. W. Martin, W. N. Mathis, R. W. McDiarmid, D. McKinnon, P. A. McLaughlin, R. F. Modlin, G. J. Morgan, S. Morris, J. C. Morse, M. Mulligan, K. Nagasawa, Dr. Nanomura, D. Nations, P. K. L. Ng, J. M. Orensanz, D. L. Pawson, M. H. Pettibone, F. Pleijel, G. Pohle, A. Raibaut, G. E. Ramos, C. B. Robbins, C. E. da Rocha, S. de A. Rodrigues, G. Rouse, E. Ruppert, D. Russell, A. V. Rybakov, C. W. Sabrosky, H. Schmalfuss, H.-K. Schminke, K. Schulz, N. J. Scott, R. Sluys, A. E. Smalley, D. G. Smith, D. Stein, D. Stewart, G. S. Steyskal, J. H. Stock, A Tsukagoshi, J. Vacelet, R. W. M. van Soest, R. P. Vari, W. Vervoort, J. L. Villalobos, J.-W. Wagele, S. H. Weitzman, M. K. Wicksten, A. B. Williams, W. W. Wirth, K. Wouters, S.-K. Wu, H. C. Yeatman, G. R. Zug.

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The World Association of Copepodologists will hold its Fifth International Conference on Copepoda at the University of Maryland, Baltimore Campus at Catonsville on 5–10 June 1993. A conference program consisting of platform presentations integrated with poster sessions and focusing on contemporary problems in copepod biology is planned. Members of the local organizing committee are: Brian P. Bradley, Chairman, Thomas E. Bowman, Frank D. Ferrari, John A. Fornshell, Janet W. Reid, T. Chad Walter, and Grace A. Wyngaard. For more information about conference topics, registration, etc. contact:

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CONTENTS

A new species of small-eared shrew, genus *Cryptotis* (Insectivora: Soricidae), from Honduras Neal Woodman and Robert M. Timm 1

A new species of *Ocadia* (Testudines: Bataguridae) from Hainan Island, China William P. McCord and John B. Iverson 13

Boehlkenchelys longidentata, a new genus and species of chlopsid eel (Teleostei: Anguilliformes) from the Indo-West Pacific region Kenneth A. Tighe 19

Jamaican Cretaceous Echinoidea (Echinodermata). 3. *Scoliechinus axiologus* Arnold and Clark, 1927, and an indeterminate cassiduloid Stephen K. Donovan 23

The flat bug genus *Calisiopsis* Champion: A review with descriptions of three new species, including one from Dominican Republic amber (Heteroptera: Aradidae) Richard C. Froeschner 32

A new genus and species of stygobiontic dryopid beetle, *Stygoparnus comalensis* (Coleoptera: Dryopidae), from Comal Springs, Texas Cheryl B. Barr and Paul J. Spangler 40

Two new crabs, *Homolopsis williamsi* and *Homolopsis centurialis* (Crustacea: Decapoda), from the Western Interior Cretaceous of the United States Gale A. Bishop 55

Miocene fossils of the genus *Cancer* (Decapoda: Cancridae) from northwestern Washington, U.S.A. James L. Goedert and Ross E. Berglund 67

A new crawfish of the genus *Orconectes* from the Yazoo River system of Mississippi (Decapoda: Cambaridae) J. F. Fitzpatrick, Jr. and Royal D. Suttkus 70

Chaceus cesarensis, a new species of fresh-water crab (Crustacea: Decapoda: Pseudothelphusidae) from Colombia with a key to the genus Gilberto Rodriguez and Angel L. Viloria 77

Redescription of *Calocarides soyoi* (Yokoya, 1933) from Japan (Crustacea: Decapoda: Axiidae) Brian Kensley and Tomoyuki Komai 81

A new geryonid crab from Walters Shoals, southwestern Indian Ocean (Crustacea: Decapoda: Brachyura) Raymond B. Manning 86

Serolis apheles, a new species (Isopoda: Serolidae) from the southwest Indian Ocean, and a range extension for *Serolis antarctica* Beddard, 1884 Marilyn Schotte 90

Description of the pelagic copepod, *Ctenocalanus heronae* Vega-Pérez and Bowman, from off São Paulo, Brazil (Calanoida: Clausocalanidae) L. Amelia Vega-Pérez and Thomas E. Bowman 97

Hyphalion sagamiense, a new species of Clausidiidae (Copepoda: Poecilostomatoida) associated with a vesicomyid bivalve from the Hatsushima cold-seep site in Sagami Bay, Japan Tatsuki Toda, Tomoyuki Miura, and Takahisa Nemoto 102

Grubeosyllis celiae, a new species of Exogoninae (Syllidae: Polychaeta) from off Ceuta, Spain Julio Parapar and Guillermo San Martín 112

On the systematic position of *Monroika africana* (Monro) (Polychaeta: Sabellidae: Fabriciinae) and a description of a new fabriciin genus and species from Australia Kirk Fitzhugh 116

Microphthalmus simplicichaetosus (Annelida: Polychaeta), a new hesionid from the northwestern American Pacific coast with exclusively simple chaetae Wilfried Westheide and Günter Purschke 132

Clausognathiidae, a new family of Gnathostomulida from Belize Wolfgang Sterrer 136

A new phylogenetic classification of the genera of the Proterodiplostomidae Dubois, 1936 (Digenea: Strigeiformes) Daniel R. Brooks, Joao Batisto Catto, and Jose F. R. Amato 143

Guide to western Atlantic species of *Cinachyrella* (Porifera: Tetillidae) Klaus Rützler and Kathleen P. Smith 148

Morphology and taxonomy of two new species of marine ciliates (Ciliophora: Spirotrichea: Stichotrichida: Amphisiellidae) Gregorio Fernandez-Leborans and Apolonia Novillo 165

International Commission on Zoological Nomenclature: Applications and Opinions 180

Reviewers—1991 182

Notices 183

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THE LUMBRINERIDS (ANNELIDA: POLYCHAETA) COLLECTED IN TWO NORTHWESTERN ATLANTIC SURVEYS WITH DESCRIPTIONS OF A NEW GENUS AND TWO NEW SPECIES

Ann B. Frame

Abstract.—Species of *Abyssoninoe, Eranno, Lumbrinerides, Lumbrineris, Paraninoe,* and *Scoletoma* (Polychaeta: Lumbrineridae) from the northwestern Atlantic are reviewed on the basis of numerous specimens collected in two long-term surveys off the east coast of the United States. The genus *Lumbrineris* Blainville is restricted; the genus *Scoletoma* Blainville is reinstated and emended; and the new genus *Lumbricalus* is erected. Two species, *Abyssoninoe winsnesae* and *Eranno petersenae,* are new to science. *Lumbrineris cingulata* (Ehlers) is newly recorded from this area and redescribed. *Scoletoma acicularum* (Webster and Benedict) is removed from synonymy with *Scoletoma fragilis* (O. F. Müller), reinstated and redescribed. *Scoletoma fragilis* is redescribed from northwestern Atlantic material. The description of *Scoletoma hebes* (Verrill) is supplemented and compared with the closely related *Scoletoma verrilli* (Perkins). *Paraninoe brevipes* (McIntosh) is redescribed and compared with *Ninoe nigripes* Verrill. *Lumbrinerides acuta* (Verrill) and *Scoletoma tenuis* (Verrill) are discussed. Key(s) are provided for the known species of *Eranno,* and for the reported northwestern Atlantic species of *Lumbrineris* and *Scoletoma.* The species of *Abyssoninoe, Paraninoe,* and *Lumbricalus* are discussed.

Problems arise in identifying specimens of *Lumbrineris* due to the large number of described species, the lack of type specimens for some of the earliest described species, incomplete descriptions by early authors, numerous instances where identification is based on tradition rather than type, and the disinclination of many to examine the pharyngeal structures. Also, at the species level there is size-dependent variability and, in some cases, variability between specimens of similar size.

Various attempts have been made to separate the known species of lumbrinerids into manageable groups. Kinberg (1865) suggested separating lumbrinerids using the dentition of maxilla III. Hartman (1944a) separated some 70 species of *Lumbrineris* s. l. first by whether the individual had composite or simple hooks, or composite spinigers, in the anterior parapodia; secondly by length and shape of posterior postsetal lobes; and then by color of the aciculae. Fauchald (1970) classified some 143 lumbrinerids first by whether they had composite hooks (and simple setae or composite spinigers in anterior parapodia), simple hooks or no hooks; second by whether they had bidentate or multidentate hooks; and third by the dentition of maxilla III.

Orensanz (1973) separated species from the axial genus *Lumbrineris* using autapomorphisms. Species with bidentate hooded hooks and simple setae were separated into the genera *Lumbrineriopsis* Orensanz, 1973 and *Lumbrinerides* Orensanz, 1973, with the former having denticulations or articulate spines on maxilla IV, and the latter lacking them. The remaining lumbrinerids were placed into four groups by setal composition. Miura (1980) further separated the known species of *Lumbrinerides* by the dentition on the inner edge of maxilla I, and *Lumbrineriopsis* by the color of aciculae. Hartmann-Schröder (1979) erected the genus *Arabelloneris* for those species without hooded hooks. Levenstein (1977) established the genus *Paraninoe* for those species having a single branchial filament on the postsetal lip of the parapodium. Orensanz (1990) further restricted '*Lumbrineris*' by differences in the maxillae, establishing the genus *Abyssoninoe* for those species with the maxilla V completely fused to maxilla IV (Fig. 3k), and reinstating and emending the genus *Eranno* Kinberg, 1865 for those species with a long strap-like basal support or plate between maxilla II and maxilla I (Fig. 4k), and with maxilla V partially fused to maxilla IV.

Following the natural system of separation of lumbrinerid genera by autapomorphisms, I here propose the following: to restrict the genus *Lumbrineris* Blainville, 1828 to species with composite hooks, simple hooks and simple limbate setae; to resurrect the genus *Scoletoma* Blainville, 1828 for species with simple hooks and simple limbate setae; and to erect the genus *Lumbricalus* for species with composite spinigers, composite hooks, simple hooks, and simple limbate setae.

Characters of diagnostic value in the Lumbrineridae.—The major diagnostic characters used to separate the lumbrinerids within a genus are: the dentition of maxillae II, III and IV (maxilla II has true teeth with internal ducts, while the teeth of maxillae III and IV are often expansions of the incisive border); the color of the aciculae; the length of the posterior postsetal lobe; the setiger on which simple hooks start in mature specimens; and the shape of maxilla IV (consistent in our species) and how it is combined with maxilla V (also known as lateral support). For purposes of illustration, maxilla IV and maxilla V are drawn on the same plane, but in reality they are part of a three-dimensional structure. Maxilla IV is a single curved piece over a muscular ridge and maxilla V is a continuation around the ridge or semicircle.

Other important characters include: the distribution and position within the parapodium of the various setae, the shape of the maxillary carriers, and the shape of the mandibles.

The number of anal cirri has been used in the literature as a means of identification. Examination of complete specimens from our surveys indicates this is frequently a size-dependent variability.

Three of our lumbrinerids have long, slender setae in the median parapodia. Hartman (1942a:117) suggests this may be an adaptation to life at great depth or to characteristics of the substratum. It is a feature easily overlooked and frequently these setae are either broken off or still present on only a few setigers.

Vascular loops should not be used as a means of identification. A vascular loop can be seen when the postsetal lobe (and sometimes the presetal lobe) is examined against background lighting, i.e., the loop shows up as lines that are lighter in color than the parapodial background. Vascular loops were found irregularly in the posterior and median regions in some mature species and can be seen in some individuals immediately and in others not until they have been preserved for a number of years. Also, these loops are more readily seen if preserved in an alcohol solution containing glycerin.

Material and methods.—Collections came from two extensive benthic surveys conducted by the National Oceanic and Atmospheric Administration: a semiannual sampling of 18–28 stations from Cape Hatteras to Nova Scotia as part of the Northeast Monitoring Program (NEMP) from 1978 to 1985 (5 grabs per station), and an annual monitoring of 44 or more stations in the New York Bight (NYB) from 1980 to 1985 (2 grabs per station). Samples were taken with a 0.1 m^2 Smith-McIntyre grab. Plastic

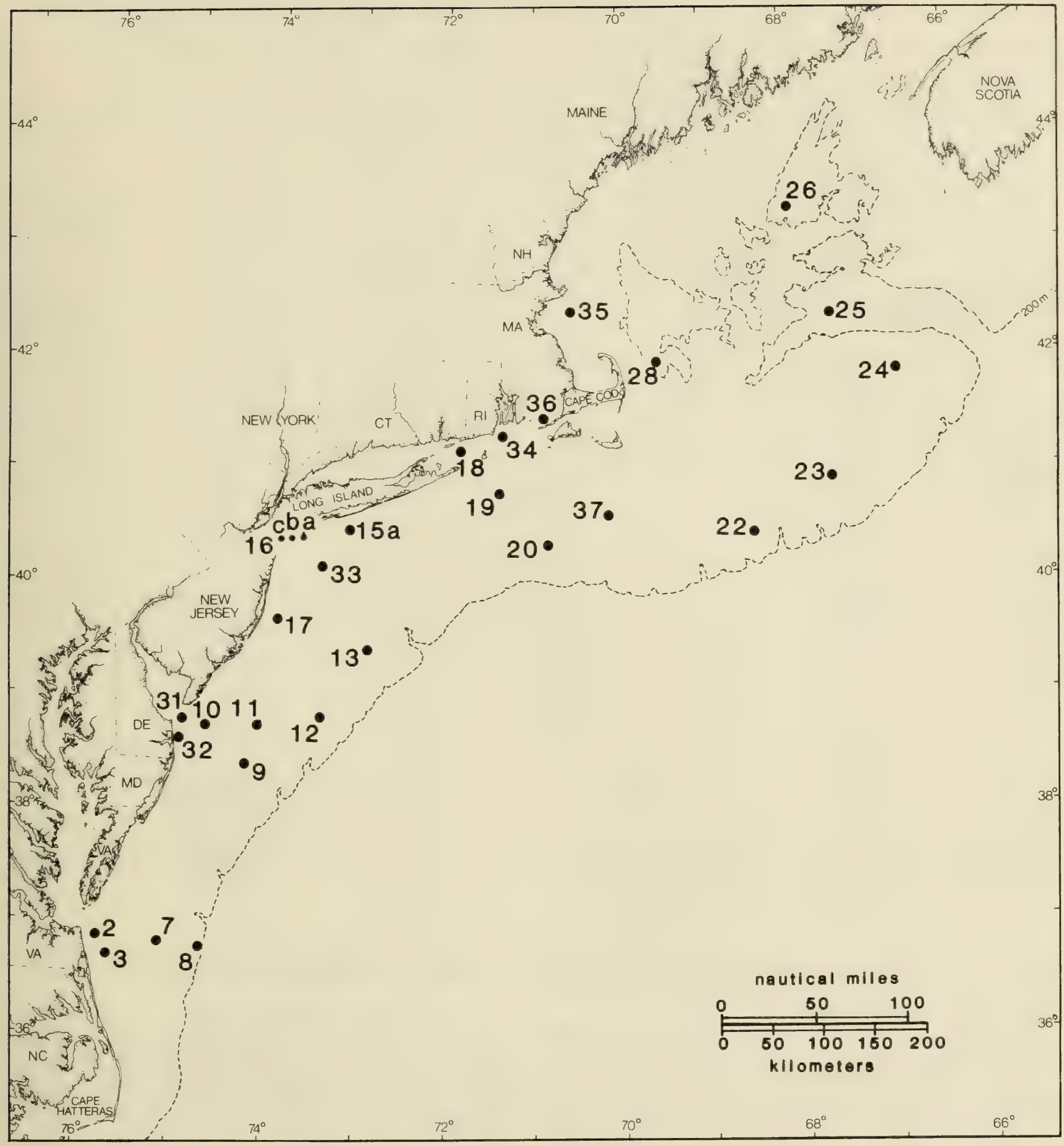

Fig. 1. Benthic stations Northeast Monitoring Program (NEMP).

tubes of 2.7 cm inner diameter were used to subsample one grab from each station for analysis of sediment grain size, organic carbon, nitrogen, and heavy metals. The remainder of the grab was rinsed through a 0.5 mm sieve, fixed in 10% buffered formalin with Rose Bengal, and transferred within one to three days to 70% ethanol with 5% glycerin. Wet weight biomass was determined by blot-drying each taxon on absorbent toweling for three minutes and weighing to the nearest mg on an electronic balance.

To date there are 1108 processed samples from the NEMP survey and 441 samples from the NYB survey. Figures 1 and 2 show the station locations. Tables 1 and 2 list station coordinates, depths, mean sediment

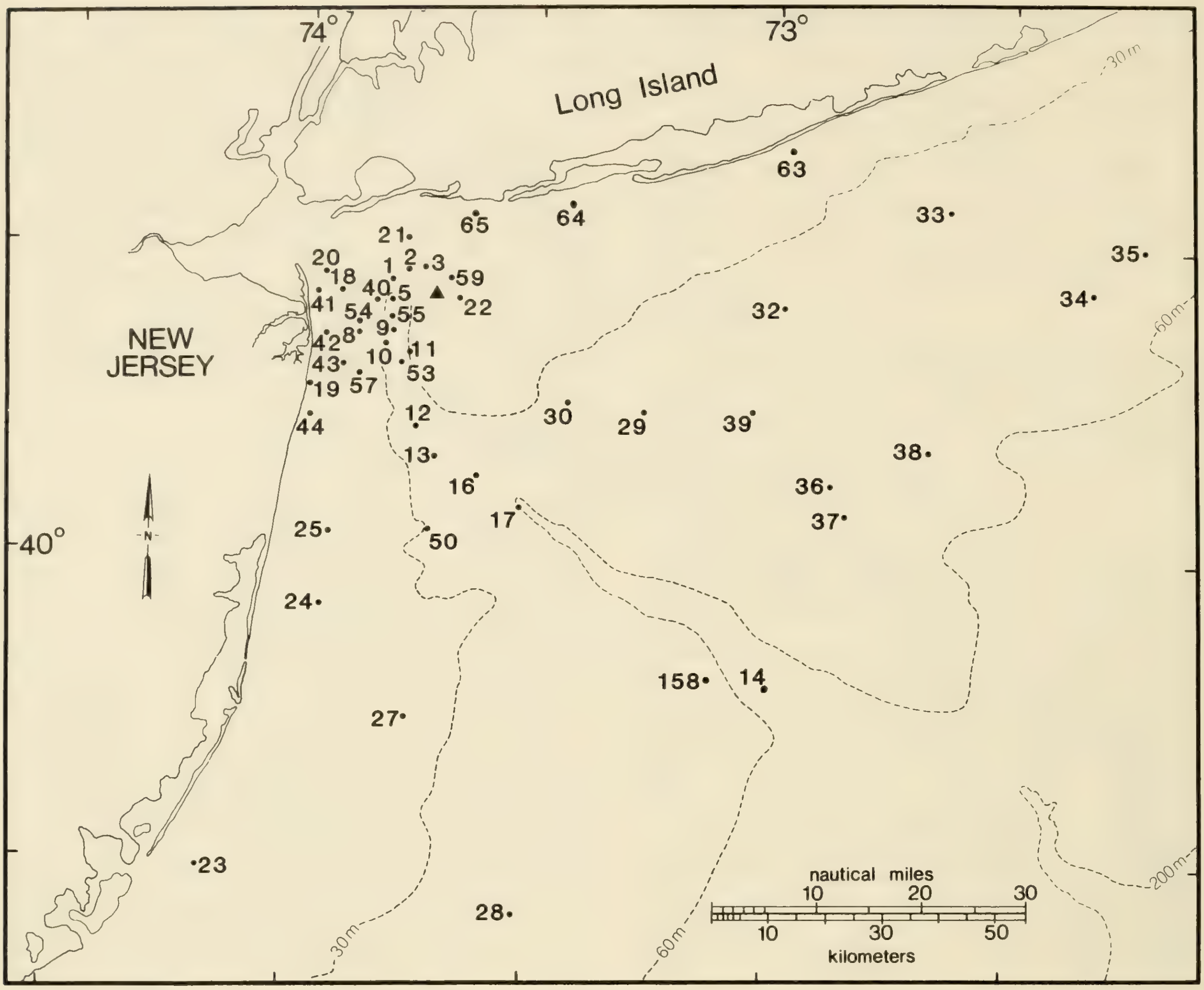

Fig. 2. Benthic stations New York Bight (NYB).

grain sizes, total organic carbon (TOC) and total Kjeldahl nitrogen (TKN).

Abbreviations used in the text and figures are as follows: bS, basal support; M, maxilla; mC, maxillary carriers; lS, lateral support; BNEMRL, Battelle New England Marine Research Laboratory; USNM, United States National Museum; ZMUC, Zoological Museum University of Copenhagen; ZMUO, Zoological Museum University of Oslo; ABF, author's personal collection.

The body width is measured on the 15th setiger (excluding parapodia) in mature species and on the 4th in juveniles. The deposit location for specimens not listed in the text is the NOAA Biological Sample Room at the Sandy Hook Laboratory, Highlands, New Jersey.

Family Lumbrineridae Malmgren, 1867

Diagnosis.—Eunicemorphs with maxillary apparatus of subprionognath structure (maxillae disposed in a semi-circle) to labidognath structure (maxillae in parallel rows). Maxillary carriers short. Five pairs of symmetrical maxillae. Maxilla I forceps-like, with pair of bridles (lateral supports) attached to its outer margin. Maxillae mineralized with calcite. Mandibles fused along symphysis, with distal calcified plate and concentric growth rings. Prostomium rounded, with 3 short occipital antennae in its pleiomorphic condition. Parapodia subbiramous, without ventral cirri, with simple limbate setae (Orensanz 1990:72).

In his 1990 monograph on the Antarctic eunicemorphs, Orensanz compared the sys-

Table 1.—Benthic Stations Northeast Monitoring Program.

Station no.	Latitude north	Longitude west	Depth (m)	Mean grain size (phi units)	TOC	TKN
					(mg/g dry wt.)	
2	36°49.8′	75°50.3′	15	1.8	3.2	0.27
3	36°33.7′	75°48.0′	20	2.56	1.38	0.22
7	36°47.5′	75°11.7′	33	1.76	0.81	0.14
8	36°40.7′	74°45.1′	80	1.57	0.78	0.07
9	38°17.3′	74°17.7′	50	1.72	1.54	0.13
10	38°44.5′	74°48.3′	23	1.61	0.76	0.10
11	38°44.6′	74°02.1′	50	2.5	1.61	0.18
12	38°46.3′	73°30.7′	70	1.95	1.89	0.21
13	39°20.4′	72°58.9′	65	1.68	2.28	0.43
15A	40°25.6′	73°11.1′	30	1.43	0.71	0.11
16A	40°25.0′	73°44.0′	25	1.86	2.42	0.21
16B	40°25.0′	73°46.0′	27	2.73	11.33	0.90
16C	40°25.0′	73°52.0′	22	2.01	3.04	0.26
17	39°35.8′	73°54.2′	28	1.29	1.03	0.08
18	41°13.5′	71°51.1′	44	3.59	6.21	0.90
19	40°41.4′	71°21.0′	62	2.05	3.01	0.46
20	40°15.2′	70°49.1′	120	6.16	15.93	1.98
22	40°30.0′	68°00.0′	110	2.52	2.76	0.41
23	40°58.0′	67°33.1′	70	2.19	1.29	0.21
24	42°17.1′	67°31.3′	260	0.97	0.48	0.06
25	42°17.0′	67°31.3′	244	2.27	3.73	0.44
26	43°14.5′	67°59.1′	51	7.732	18.67	2.73
28	41°50.6′	69°30.0′	187	7.93	13.09	2.11
31	38°44.8′	75°01.0′	25	1.14	8.31	1.28
32	38°31.4′	74°57.9′	15	1.4	0.74	0.08
33	40°01.4′	73°25.6′	62	3.31	8.35	1.03
34	41°24.0′	71°25.0′	32	5.6	9.77	1.20
35	42°19.0′	70°36.0′	60	5.27	8.6	1.06
36	41°29.0′	70°53.0′	23	6.78	17.92	2.19
37	40°29.7′	70°12.2′	60	4.77	10.28	1.28

tematics and phylogeny of families by their complex maxillomandibular pharyngeal armature. He considered as secondary losses in the family Lumbrineridae: the loss of maxillae V in some genera, the loss of antennae in most genera, and the notopodia reduced or absent (uniramous parapodia) in most genera.

Genus *Abyssoninoe* Orensanz, 1990

Type species.—*Lumbriconereis abyssorum* McIntosh, 1885; designated by Orensanz, 1990.

Diagnosis.—Prostomium conical. Parapodia uniramous with simple limbate setae and simple, multidentate hooded hooks. Hooded hooks may have a transitional phase, evolving through anterior setigers from rounded tip limbate setae, to faintly outlined hooks, to clearly defined hooks and teeth. M V completely fused to M IV, forming a broad semicircular plate with a tooth protruding from the middle of the inferior border. M III unidentate. Aciculae yellow. 1–2 pairs of anal cirri, if 2 pair dorsal cirri longer than ventral.

Abyssoninoe winsnesae, new species

Fig. 3

Material examined.—Northwestern Atlantic, Off NE U.S.A.: NEMP Sta. 20, 15 July 1981 (1 ABF); NEMP Sta. 25, 2 May

Table 2.—Benthic Stations New York Bight.

Station no.	Latitude north	Longitude west	Depth (m)	Mean grain size (phi units)	TOC	TKN
					(mg/g dry wt.)	
1	40°26.9′	73°48.1′	27	3.71	9.4	1.1
2	40°28.2′	73°45.8′	29	3.35	10.1	1.4
3	40°28.0′	73°43.8′	28	3.43	7.1	0.83
5	40°24.9′	73°48.0′	35	4.19	16.0	1.9
8	40°21.8′	73°51.6′	24	2.37	34.0	1.5
9	40°21.6′	73°47.8′	36	3.49	13.0	1.5
10	40°20.2′	73°49.1′	61	−0.24	1.6	0.17
11	40°19.1′	73°45.8′	31	3.3	5.1	0.71
12	40°12.8′	73°44.0′	38	3.29	5.5	0.70
13	40°09.8′	73°41.9′	56	4.25	11.0	1.8
14	39°47.3′	72°59.0′	74	2.01	4.9	0.73
16	40°07.6′	73°36.8′	71	4.68	15.0	2.2
17	40°05.4′	73°31.3′	73	3.62	11.0	1.5
18	40°25.0′	73°53.8′	24	2.2	14.0	1.1
19	40°16.0′	73°57.8′	14	1.76	0.86	0.15
20	40°27.9′	73°56.0′	12	1.96	0.95	0.17
21	40°31.1′	73°45.9′	21	3.15	12.0	1.5
22	40°25.0′	73°39.8′	24	3.07	2.4	0.36
23	39°29.9′	74°10.1′	16	1.01	0.46	0.09
24	39°55.0′	73°55.8′	18	−0.52	1.8	0.12
25	40°01.9′	73°55.1′	19	0.26	0.49	0.08
27	39°44.7′	73°44.9′	26	1.21	0.58	0.10
28	39°25.5′	73°30.6′	40	2.27	0.82	0.13
29	40°14.3′	73°15.9′	38	1.09	0.63	0.13
30	40°14.8′	73°25.1′	34	1.86	0.81	0.16
32	40°24.2′	72°58.3′	38	1.19	0.51	0.14
33	40°34.1′	72°37.8′	40	2.37	1.8	0.29
34	40°25.8′	72°19.8′	54	1.77	3.4	0.46
35	40°30.2′	72°13.1′	55	2.43	3.9	0.69
36	40°08.1′	72°51.6′	56	1.19	0.81	0.15
37	40°04.9′	72°50.2′	54	1.41	1.0	0.17
38	40°10.7′	72°40.3′	56	1.05	1.1	0.17
39	40°14.3′	73°02.0′	42	1.42	0.79	0.12
40	40°24.9′	73°49.7′	29	3.35	12.0	1.5
41	40°25.0′	73°56.8′	21	1.25	0.3	0.05
42	40°21.2′	73°56.6′	13	0.27	3.4	0.36
43	40°18.9′	73°53.7′	20	−0.19	1.1	0.12
44	40°13.0′	73°57.8′	19	−0.2	2.6	0.17
63	40°39.5′	73°00.0′	12	1.04	0.8	0.02
64	40°35.5′	73°22.0′	11	2.28	0.5	0.02
65	40°33.2′	73°37.5′	11	−0.61	0.86	0.03
158	39°46.2′	73°08.2′	48	0.86	1.3	0.03

1978 (4 ABF); NEMP Sta. 28, 17 Dec 1980 (28 ABF), 20 Jul 1981 (1 paratype USNM 146097, 45 paratypes ZMUO, 155 ABF), 28 Jan 1982 (29 paratypes USNM 146098, 25 ABF), 5 Jul 1983 (holotype USNM 146099, 4 paratypes USNM 146100, 1 USNM 146101, 76 ABF), 4 July 1984 (26 paratypes ZMUC, 42 ABF); NEMP Sta. 35, 21 Jul 1981 (5 ABF), 29 Jan 1982 (1 ABF).

Description.—Preserved material colorless to light tan, except for single specimen with transverse brown stripe across each se-

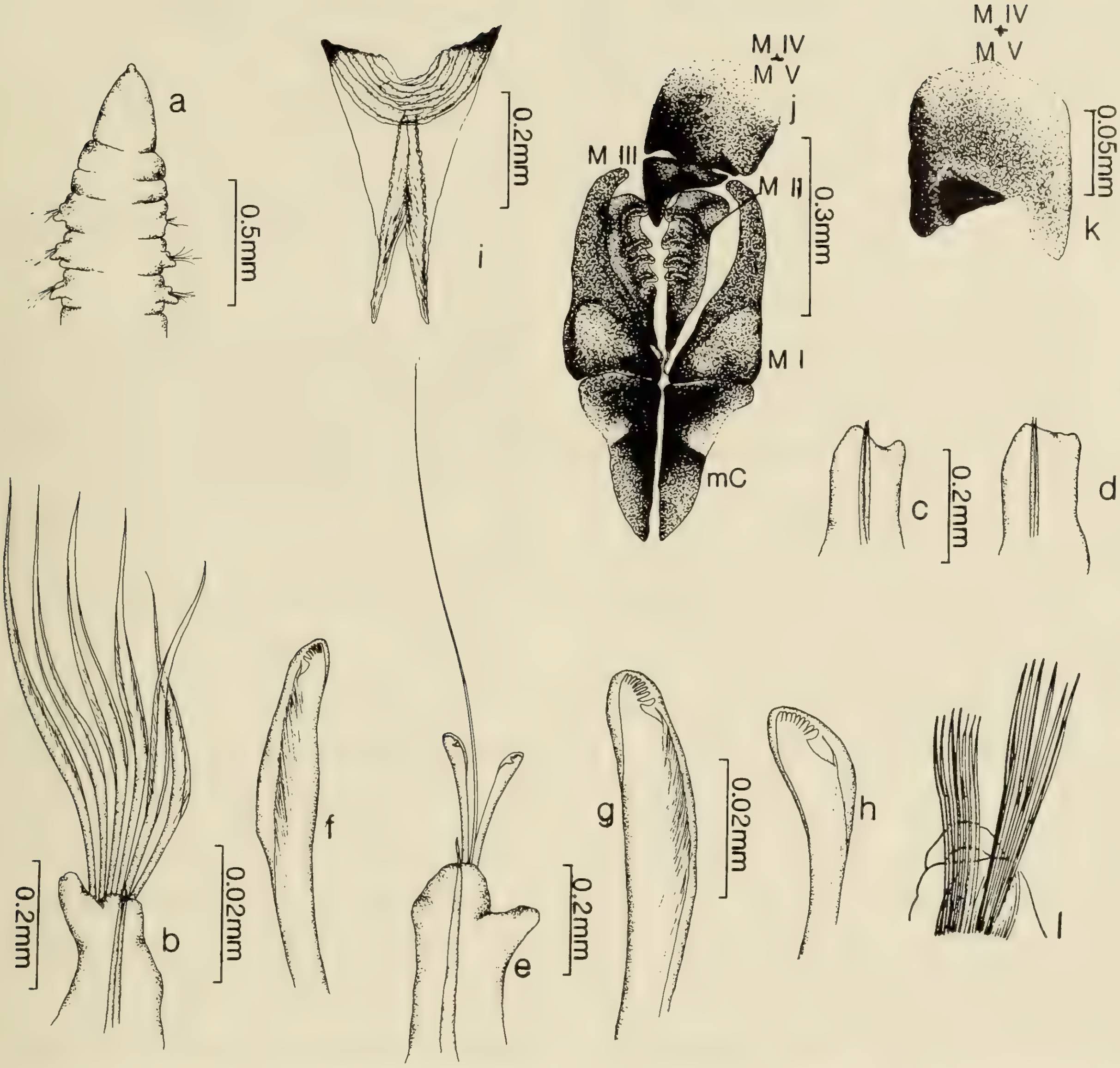

Fig. 3. *Abyssoninoe winsnesae*: a, Prostomium; b, Left parapodium 1; c, Parapodium 22, hooks and setae omitted; d, Parapodium 37, hooks and setae omitted; e, Parapodium 52; f, Hooded hook from parapodium 14; g, Hook from parapodium 47; h, Hook from parapodium 79; i, Mandibles; j, Maxillae; k, Left M IV fused with lateral support, dorsolateral view. *A. hibernica* (McIntosh, 1903): 1, Parapodium 1 (from McIntosh 1910, pl. 74, fig. 1).

tiger, and setiger more beadlike in anterior region (USNM 146101). Largest specimen (incomplete) 22 mm long, 1.1 mm wide, with 51 setigers. Largest whole specimen 13 mm long, 0.75 mm wide, with 102 setigers. Prostomium (Fig. 3a) longer than wide, acorn-shaped with mammiform extension of prostomium in freshly preserved material, with prostomium extension becoming less distinct after being preserved 6–12 months. Peristomial segments similar in width to first setiger, each about as long as first setiger. Body width uniform to about setiger 64, then tapering towards posterior end; setigers wider than long anteriorly, becoming moniliform posteriorly. Postsetal lobes of anterior parapodia small, conical to setiger 8–12 (Fig. 3b); decreasing in size, not exceeding parapodium, appearing mitten-shaped (Fig. 3c); median parapodia without a distinct shape (Fig. 3d), then again appearing mitten-shaped; posterior lobes small, conical. Presetal lobes not distinguishable. 1 or 2 pairs of anal cirri: if 2 pairs, long dorsal and short ventral cirri. Pygidium rounded anal disc in a juvenile 4.2 mm long by 0.3 mm wide with 38 setigers. Anterior parapodia with 5–6 (rarely 7–8) bilimbate setae, single superior seta longest, others of random length. Bilimbate setae number decreasing after setiger 8, totally lacking after setiger 20. From about setiger 17–35 (22–52 in large ovigerous female) parapodia with 1–2 very long, slender, capillary setae with whiplike tips, setae twice as long as anterior bilimbate setae (Fig. 3e). Simple hooded hooks starting on setiger 8–12, with 1–3 per parapodium. Hooks slender, of medium length in anterior setigers (Fig. 3f) becoming wider and more elongated in median region (Fig. 3g), bulbous posteriorly (Fig. 3h). Each hook with 6–8 teeth of equal size, with main fang only slightly larger. Aciculae yellow, 3 present in anterior parapodia decreasing to 1 in posterior parapodia, each with long, thin tip projecting through parapodial wall.

Mandibles translucent, fused for two thirds of their length (Fig. 3i). Maxillary apparatus of medium hardness. Maxillary carriers broad, slightly constricted in middle, permanently divided; M I base broad, tips falcate; M II with 4 (rarely 3) teeth, with space between distal teeth; M III unidentate; M IV large, with a short conical tooth at fusion with M V (Fig. 3j). M V completely fused to M IV, appearing as broad semicircular plate with tooth protruding from middle of inferior border (Fig. 3k).

Remarks.—In addition to *A. winsnesae,* the genus *Abyssoninoe* includes the following species:

Lumbriconereis abyssorum McIntosh, 1885; Antarctic, Peru-Chile trench off Chile, fjords of New Zealand and Norway, Gulf of Gascogne, off Congo, and Mediterranean Sea; 274–6000 m.

Lumbriconereis hibernica McIntosh, 1903; Clyde Sea; 49–70 m (Winsnes, pers. comm.).

Lumbrineris galatheae Knox & Green, 1972; New Zealand; 23–1000 m.

Lumbrineris scopa Fauchald, 1974; Hardangerfjorden, fjords of W Norway and Trondelag; 200–395 m.

Lumbrineris scopa aequilobata Winsnes, 1981; fjords of W Norway and Trondelag; 20–340 m.

Lumbrineris cf. *scopa* (Miura, 1980); Bay of Biscay, off Congo, and Mediterranean Sea; 1163–2742 m.

All the known species of *Abyssoninoe* have a unidentate M III and yellow aciculae. *Abyssoninoe abyssorum* has transitional hooded hooks starting on setiger 1, with the teeth becoming clearly defined by setiger 10–18; 4 teeth on M II; and the postsetal lobes are short and conical throughout. Orensanz (1990:76) examined *L.* cf. *scopa* sensu Miura and placed it in synonymy with *A. abyssorum.* He considers *A. galatheae* to be a presumable synonym of *A. abyssorum,* but the type material was not available for study. *Abyssoninoe scopa* has transitional hooks becoming clearly defined by setiger 20, 5 teeth on M II, and long postsetal lobes posteriorly. *Abyssoninoe scopa aequilobata* has transitional hooks becoming clearly defined by setiger 15, 5 teeth on M II, and bilabiate parapodia posteriorly. *Abyssoninoe winsnesae* is closest to *A. hibernica.* Both have hooks starting in the same area (*A. winsnesae* setigers 8–12 and *A. hibernica* 10–16, see Clark 1952:11), 4 teeth on M II, and very long, slender capillary setae in some of the median setigers. However, *A. hibernica* has low, gently rounded, triangular postsetal lobes in the anterior setigers, instead of small conical ones; and the anterior parapodia have two setal groups with the superior group longer than the inferior (copied as Fig. 3l), instead of a longest superior seta and the others of random length.

Distribution.—Gulf of Maine to 150 km south of Rhode Island; 110–224 m. Grain size range from granular to coarse clay; greatest numbers in fine sand. TOC values from 0.8–14.9 mg/g.

Etymology.—This species is named in honor of Dr. Inger M. Winsnes in recognition of her scientific papers on the family Lumbrineridae.

Genus *Eranno* Kinberg, 1865

Type species.—*Eranno bifrons* Kinberg, 1865; reinstated and emended by Orensanz, 1990.

Diagnosis.—Prostomium conical. Parapodia uniramous with simple limbate setae and simple, multidentate hooded hooks. Mandible shafts long. M II proportionally short (about ½ the length of M I), connected to M I by broad basal supports or plates. M V partially fused to M IV.

Eranno petersenae, new species
Fig. 4

Material examined.—Northwestern Atlantic, Off NE U.S.A.: NEMP Sta. 19, 15 Jul 1980 (5 ABF), 27 Jan 1982 (1 paratype USNM 146102, 7 ABF); NEMP Sta. 20, 27 Sep 1978 (1 ABF), 10 Dec 1980 (1 ABF), 15 Jul 1981 (holotype USNM 146103).—Northwestern Atlantic, Off New Jersey (1 paratype USNM 146104): coll. BNEMRL, Duxbury, Massachusetts, BNEMRL *Lumbrineris* sp. 2, B. Hilbig ID.

Description.—Preserved material light tan to pinkish tan, slightly iridescent. Largest ovigerous female (incomplete) 78 mm long, 2 mm wide, with 138 segments. Largest anterior fragment 2.5 mm wide. Prostomium (Fig. 4a) short, conical, about as long as wide. Peristomial segments similar in length to setiger 1 and only slightly narrower. Body width uniform to about setiger 87, then tapering posteriorly; anterior setigers much wider than long, becoming subequal. Postsetal lobes of anterior parapodia low, obliquely truncate, flaplike to about setigers 18–21 (Fig. 4b); narrowing and becoming obliquely conical in median parapodia (Fig. 4c); digitate and elongated in posterior ones. Presetal lobes low, round, wider than postsetal lobes, with faint notopodial rudiment in anterior and median setigers; digitate, shorter than postsetal lobe in posterior ones, forming a bilabiate parapodium (Fig. 4d). Two small specimens with single lobe pygidia.

Anterior parapodia with up to 11 bilimbate setae, greatest numbers of setae occurring on setigers 7–11, setae less numerous after setiger 11 (1–2), disappearing by setigers 60–70. Setiger 9 with 9 bilimbate setae, 9 hooded hooks followed by 2 bilimbate setae. Specimens 2 mm wide with one or more long, slender bilimbate setae with whiplike tips on setigers 22–67 (17–96). Setiger 45 with single short seta, 2–3 long, slender setae, and 2–3 bulbous hooks. Slender, long bladed hooks present from setiger 1, hooks bulbous in median and posterior setigers. All hooks with a subdivided main fang; above fang, a singular tooth standing distinctly by itself. Above singular tooth, anterior hooks with 4–7 teeth of equal size (Fig. 4e); hooks in median (Fig. 4f–g) and posterior setigers (Fig. 4h–i) with teeth varying widely in number and shape. Aciculae yellow, up to 6 in anterior parapodia, 2–3 in posterior ones. Aciculae bluntly conical with long acute tips protruding through parapodial wall. Vascular loops sometimes present in presetal and postsetal lobes.

Mandible blades (Fig. 4j) long and slender, fused for half their length. Maxillary apparatus hard. Maxillary carriers long (Fig. 4k); M I forceps long; M II short, half the length of M I, with 4 or 5 asymmetrically arranged teeth, distal tooth largest, M II attached to M I by long broad basal support in addition to small connecting membrane (broken in Fig. 4k); M III unidentate; M IV with single irregular tooth, plate deeply incised above tooth, M V attached at upper edge of incision (Fig. 4i). M V like thick comma; from where attached, it extends basally until it loops, at right angle, around inferior edge of M III's tooth (M III, M IV, and M V separated for purposes of illustration).

Remarks.—In addition to *E. petersenae,* the genus *Eranno* includes the following species:

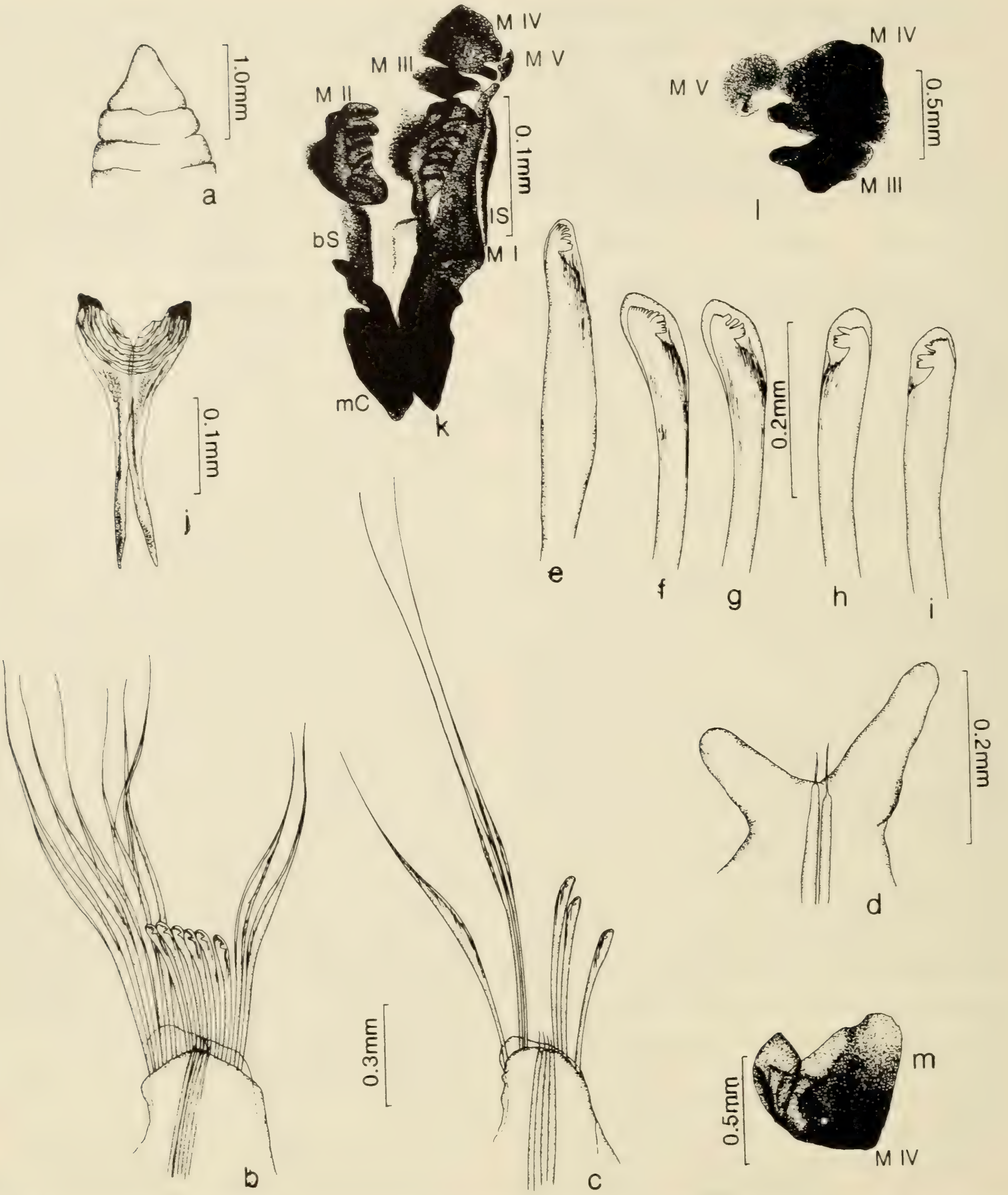

Fig. 4. *Eranno petersenae*: a, Prostomium; b, Right parapodium 4; c, Parapodium 45, BNEMRL specimen; d, Posterior parapodium; e, Hooded hook from parapodium 6; f–g, Hooks from parapodium 45; h–i, Hooks from posterior parapodium; h, Mandibles; i, Maxillae; j, Left M III, M IV and M V. *Eranno lagunae* (Fauchald, 1970): k, Right M IV (USNM 19405).

Lumbriconereis abyssicola Ushakov, 1950; Sea of Okhotsk; 3500 m.

Lumbriconereis bifilaris Ehlers, 1901; Chile.

Lumbriconereis bifrons (Kinberg, 1865); southwestern Atlantic, South Sandwich Islands, North Atlantic, Irish Sea, Gulf of Gascogne, off Congo; 52–5121 m.

Lumbriconereis bifurcata (McIntosh, 1885);

Japan, Sea of Okhotsk, Pacific coast of North America; 592–1643 m.

Lumbriconereis chilensis Kinberg, 1865; off Valparaiso.

Lumbriconereis ehlersii (McIntosh), 1885; Greenland.

Lumbriconereis ehlersii tenuisetis (McIntosh, 1885); northwestern Atlantic, midway between Halifax and New York; 2352 m.

Lumbrineris impatiens antarctica (Averincev, 1972); Antarctic.

Lumbrineris lagunae (Fauchald, 1970); western Mexico, California; subtidally–49 m.

Key to the species of *Eranno*

1\. Maxillae III unidentate 2
– Maxillae III bidentate 5
2\. Maxillae more than ½ the length of maxillae II, aciculae black, hooks starting on setiger 7, posterior parapodia bilabiate .... *E. bifurcata*
– Maxillae II less than ½ the length of maxillae II, aciculae yellow, hooks starting on setiger 1, posterior parapodia may be bilabiate 3
3\. Posterior parapodia with short conical postsetal lobes ....*E. bifrons*
– Posterior parapodia lobes bilabiate 4
4\. Maxillae V overlaps maxillae IV .. ..*E. lagunae*
– Maxillae V does not overlap maxillae IV ....*E. petersenae*
5\. Maxillae IV with 4 sawlike teeth .... *E. bifilaris*
– Maxillae IV with 1 tooth 6
6\. With some of the parapodia bilabiate, maxillae I with 4 teeth .... *E. chilensis*
– Without some of the parapodia bilabiate, maxillae II with 5–6 teeth .... *E. abyssicola*

Orensanz (1990:78) considers as synonyms of *E. bifrons*: *E. ehlersii* McIntosh, 1885; *E. ehlersii tenuisetis* McIntosh, 1885 (fide Miura 1980); *E. impatiens antarctica*. *E. petersenae* is very similar to *E. lagunae*. Examination by the author of the paratype of *E. lagunae* (Gulf of California, Sta. 3435, 859 fms, 22 Apr 1891 (1), K. Fauchald ID, 1970, USNM 19405) reveals that M V overlaps M IV (Fig. 41), and the tooth is a small knob on the maxilla surface (white in the figure). Also, *E. lagunae* has 1 aciculum per parapodium instead of 6 in anterior and 2–3 in posterior segments; its bilabiate parapodial lobes are about twice the length of *E. petersenae*; the digitate presetal lobes are present in the median region (setiger 65), instead of only in the posterior, and the mandibles are X-shaped with blades wide apart instead of long slender blades fused for half their length.

Distribution.—50–125 km south of Rhode Island; 62–120 m. Grain size range from fine sand to fine silt, greatest numbers in fine silt. TOC values from 3.2–17.6 mg/g. Present at BNEMRL from offshore stations from New Jersey to New England, in low but consistent numbers, 800–2000 m, in fine sand to clay.

Etymology.—This species is named in honor of Dr. Mary E. Petersen in appreciation for her help in providing the information on O. F. Müller's type locality for *Lumbrineris fragilis*, and for providing the historical background and original descriptions of European lumbrinerids.

Lumbricalus, new genus

Type species.—*Lumbriconeris januarii* Grube, 1878.

Diagnosis.—Prostomium conical. Parapodia uniramous, may have a notopodial rudiment. Parapodia with composite spinigers; composite, multidentate hooded hooks (usually); simple limbate setae; and simple, multidentate hooded hooks. M III with up to 5 small teeth, M IV unidentate, M V free standing, displaced outward to M IV.

A typical fascicle is composed of a superior limbate seta, composite spinigers, followed by 1–2 composite hooks, and limbate setae.

Remarks.—Hartman (1944a:167) examined and redescribed the type specimens of *Lumbriconeris januarii* Grube, 1878. M III was described as having 4–5 fine dentitions on its broad cutting edge, and M II having 5 teeth. As *Lumbriconeris brasiliensis* Kinberg, 1865 was the only species Hartman knew which had compound spinigerous setae, she proposed that *L. brasiliensis* be considered a synonym of *L. januarii* (Grube, 1878). Hartman (1948:93) later examined Kinberg's type species of *L. brasiliensis* and found it lacked mouthparts. Day (1973:62) briefly described and called a second species *L. januarii* which has a bidentate maxilla III. Uebelacker (1984:Ch. 41, pp. 32, figs. 30a–i) has an excellent description and figures of this species. It is proposed that *L. januarii* sensu Day be renamed *Lumbricalus dayi* in honor of Professor J. H. Day, who collected and first reported this species from North Carolina.

The following species are included in this genus:

Lumbriconereis adriatica Fauvel, 1940; Adriatic Sea, Mediterranean Sea, Senegambia, and Congo; 65–1163 m.

Lumbriconereis adriatica foresti Fauvel & Rullier, 1959; Adriatic Sea.

Lumbrineris aotearoae Knox & Green, 1972, New Zealand; shallow depths to 150 m.

Lumbriconereis brasiliensis Kinberg, 1865; Rio de Janeiro, Brazil.

Lumbrineris composita Hartmann-Schröder, 1965; Chile.

Lumbrineris cultriformis Intes & Le Loeuff, 1975; Ivory Coast, Africa; 80 m.

Lumbricalus dayi; new name proposed for *Lumbrineris januarii* sensu Day, 1973; North Carolina to Gulf of Mexico; 10–168 m.

Lumbriconereis januarii Grube, 1878; Tobago, West Indies.

Miura (1980:1035) examined the types of *L. adriatica* and *L. adriatica foresti* and considered *L. adriatica foresti* a synonym of *L. adriatica*. *Lumbricalus aotearoae* and *L. composita* have a unidentate M III. *Lumbricalus aotearoae* has a greater number of setae in anterior parapodia, 19 or more as opposed to 9; and lacks the long posterior postsetal lobe of *L. composita*. *Lumbricalus cultriformis, L. adriatica,* and *L. dayi* have a bidentate M III. *Lumbricalus cultriformis* lacks compound hooks and its simple hooks have 5 teeth. *Lumbricalus adriatica* simple hooks have 5–6 teeth, while *L. dayi* simple hooks have 9 teeth. *Lumbricalus januarii* M III has a broad edge with 4–5 fine dentitions. In Kinberg's (1865:570) description of *L. brasiliensis,* M II has 2 teeth, M IV has 1 tooth, while M III is not mentioned.

Lumbrinerides Orensanz, 1973

Type species.—*Lumbrinerides gesae* Orensanz, 1973.

Diagnosis.—Prostomium long, distally pointed. Parapodia uniramus with simple bidentate hooded hooks, and simple limbate setae. Maxillary carriers large, triangular, broad anteriorly. M I usually with 1–2 accessory teeth on inner margin, mandibles usually fused for entire length. Aciculae yellow or black.

Lumbrinerides acuta (Verrill, 1875)

Lumbriconereis acuta Verrill, 1875:39, pl. 3, fig. 5.

Lumbrineris acuta.—Hartman, 1942b:114, fig. 10a–d.—Pettibone, 1963:260, fig. 67g–i.—Perkins, 1979:419, fig. 1a.

Lumbrinerides acuta.—Orensanz, 1973: 371.—Gardiner, 1976:203, fig. 26i–l (in part, New England specimens).—Perkins, 1979:419, fig. 1a.—Miura, 1980:1023.—Uebelacker, 1984:Ch. 41, pp. 11–13, figs. 7, 8a–g.

Material examined.—Northwestern Atlantic, Off NE U.S.A.: Numerous specimens, with 70 records at NEMP Stations 2, 7–13, 17, 19–20, 22, 24, 32–34, 36–37, 15A, 16C; and 155 records at NYB Stations 1, 8, 10–16, 18–19, 21, 24, 27–34, 36–44, 63, 65.

Remarks.—Orensanz (1973:373) referred 6 species to the genus *Lumbrinerides.* Perkins (1979:417) provided a key to 10 species of *Lumbrinerides.* His fig. 1a of the maxillary apparatus of *L. acuta* was drawn from the USNM syntype 12895. Miura (1980:1023) provided a key to 14 species of *Lumbrinerides.*

Lumbrinerides acuta may be distinguished from other *Lumbrinerides* by its having: the accessory tooth of M I as large as the distal tooth and located close to it; 3 teeth on M II; hooded hooks beginning in the middle setigers; and 2 visible peristomal segments.

Distribution.—Georges Bank to Gulf of Mexico; 14–260 m. Grain size range from coarse silt to pebble, greatest numbers in coarse silt to fine sand. TOC values from 0.3–32.6 mg/g.

Lumbrineris Blainville, 1828

Type species.—*Lumbrineris latreilli* Audouin & Milne Edwards, 1833; designated by Hartman, 1959.

Diagnosis.—Prostomium conical or globular, usually without papillae, occasionally with a single papilla in nuchal fold. Parapodia uniramous, sometimes with a notopodial rudiment. Parapodia with composite, multidentate hooded hooks in the anterior parapodia; simple limbate setae, and simple, multidentate hooded hooks. M III and IV usually unidentate or bidentate. M V free standing, displaced outward to M IV. Aciculae yellow or black, of light color in juveniles.

Historical background.—Blainville, author of the "Mollusques, Vers and Zoophytes" sections in the 1828 Dictionnaire des Sciences Naturelles, established the genera *Lumbrineris* (pp. 486–487) and *Scoletoma* (p. 492). In his system of classification, Blainville placed *Lumbrineris,* because of its buccal armature, among the multidentate nereids. He established the genus *Lumbrineris* for two large and beautiful 'chaetopoda,' *L. brillant* and *L. scolopendrina,* that he had in his collection, but was uncertain of their place of origin. Blainville goes on the say, "we are assured by a more detailed examination of what we had described in the dictionary and named the anus, is certainly the mouth." He also placed within this genus *Nereis ebranchiata* Pallas, 1788. According to Hartman (1959:336–337) these three species are "indeterminable." Blainville established the genus *Scoletoma* for *Lumbricus fragilis* O. F. Müller, 1776. Blainville states, "we do not believe we have seen this chaetopoda, but it could be one of the two species of *Lumbrineris.* However, the number of segments were less in the two [*Lumbrineris*], and neither one of them could be considered fragile."

Audouin & Milne Edwards (1833:216) placed *Lumbrineris* within the family Eunicae Savigny, 1818 (Eunicidae) and separated the genera by whether or not they had branchiae. They described the new species *L. latreilli* from the Chaussey Islands, placed within this genus *Nereis coccinea* Renier, 1804 from the Mediterranean (pp. 242–244), and commented on other lumbrinerids (indeterminable or placed in other genera). Audouin & Milne Edwards combined *Scoletoma* with *Lumbrineris* because it seemed probable that when *S. fragilis* was better studied, it would be placed within this group. But they go on to say, "in the actual state of science, this annelid is too poorly known for us to have a definite opinion."

Grube (1840:79) listed *L. quadristriata* (*Arabella iricolor*), *L. Nardonis* (*L. latreilli*) and *L. unicornis* (*Nematoneris unicornis*) under *Lumbriconereis* Blainville (a misspelling of *Lumbrineris*). Treadwell (1921: 94) noted that the original name was *Lumbrinereis* and not the *Lumbriconereis.* However, he used delle Chiaje's (1841) spelling (-reis) not Blainville's (-ris). Moore (1900: 458) noted the name was usually erroneously written as *Lumbrinereis* or *Lumbri-*

coneris. Hartman (1944a:136) reinstated Blainville's spelling and listed the type (in general usage) as *Lumbrineris fragilis* O. F. Müller. However, in 1959 (p. 333) Hartman listed all the synonyms and variant spellings of *Lumbrineris,* and indicated *Lumbrineris latreilli* Audouin & Milne Edwards as the type species.

Given that (a) all the species originally included in the genus *Lumbrineris* by Blainville (1828) are indeterminable (Hartman 1959), (b) that their types probably no longer exist, and (c) that *L. latreilli* Audouin & Milne Edwards cannot be the type species according to the ICZN third edition articles 67.h and 69.a.i, the definition of *Lumbrineris* is uncertain. The ICZN 1990 meeting proposed a fourth edition in which procedures would be adopted that validate names in current use rather than those following strict priority. I use the *Lumbrineris* according to this paper's genus diagnosis, with the warning that a new name may have to be created, or a junior synonym may have to be revised and redefined.

According to the literature the following species of *Lumbrineris* s. s. are present from the northwestern Atlantic in addition to the ones found in this study: *L. coccinea* (Renier, 1804); *L. cruzensis* Hartman, 1944; *L. inflata* Moore, 1911; and *L. latreilli* Audouin & Milne Edwards, 1833.

Key to the Northwestern Atlantic species of *Lumbrineris*

1. Maxillae III unidentate 2
– Maxillae III bidentate 3
– Maxillae III multidentate ... *L. inflata*
2. Posterior parapodia bilabiate, postsetal lobe long and slender *L. cruzensis*
– Posterior parapodia unilabiate, postsetal lobe short .... *L. cingulata*
3. Blades of composite hooks of similar length throughout; prostomium short, globular or round ... *L. coccinea*
– Blades of composite hooks longer in anterior parapodia; prostomium conical .... *L. latreilli*

Lumbrineris cingulata (Ehlers, 1897)
Fig. 5

Lumbriconereis cingulata Ehlers, 1897:76, pl. 5, figs. 119–124; 1901:136.—Fauvel, 1936:22.

Lumbriconereis virgini.—Kinberg, 1865:568 (in part).

Lumbriconereis magalhaensis.—Ehlers, 1900:215; 1901:136 (in part).

Lumbrinereis magalhaensis.—Monro, 1930 (in part, st. DISC/51); 1936:53 (in part, WSCO/215 and WSCO/856).

Lumbrinereis cingulata.—Wesenberg-Lund, 1962:215.

Lumbrineris cingulata.—Hartman, 1964: 121, pl. 37:figs. 5–6.—Orensanz 1973:361–365, pls. 7–8; 1976:38; 1990:82–85, pls. 21, 22:figs. a–f, chart 4C.

Lumbrineris patagonica.—Hartmann-Schröder, 1962:119, figs. 124–127.

Lumbrineris limbata.—Hartmann-Schröder, 1965:178, figs. 153–156.

Material examined.—Northwestern Atlantic, Off NE U.S.A.: NEMP Sta. 8, Dec 15 1979 (10 ABF), 20 Jul 1980 (10 ABF), 7 Dec 1980 (19 ABF), 12 Jul 1981 (2 ABF), 8 Feb 1982 (13 ABF), 30 Aug 1982 (5 ABF), 10 Jul 1983 (1 ABF); NEMP Sta. 11, 29 Aug 1982 (10 ABF); NEMP Sta. 13, 17 Dec 1979 (1 ABF); NEMP Sta. 19, 15 Jul 1980 (2 ABF), 10 Dec 1980 (3 ABF), 2 Sep 1982 (11 ABF); NEMP Sta. 20, 28 Apr 1978 (3 ABF), 19 Sep 1979 (1 ABF), 11 Dec 1979 (19 ABF), 10 Dec 1980 (4 ABF), 15 Jul 1981 (3 ABF), 28 Aug 1982 (2 ABF), 5 Jul 1984 (4 ABF); NEMP Sta. 22, 30 Apr 1978 (38 ABF), 28 Sep 1978 (12 ABF), 24 Jul 1979 (15 Orensanz, 12 ABF), 17 Sep 1979 (24 ABF), 11 Jul 1980 (8 ABF), 18 Dec 1980 (2 USNM 146105, 64 ABF), 17 Jul 1981 (212 ABF), 31 Jan 1982 (134 ABF), 27 Aug 1982 (1 USNM 146106, 81 paratypes ZMUC, 72 paratypes ZMUO, 44 ABF), 18 Jul 1984 (88

USNM 146107, 45 ABF); NEMP Sta. 25, 2 May 1978 (2 ABF); NEMP Sta. 28, 4 Dec 1979 (82 ABF), 17 Dec 1980 (21 ABF), 20 Jul 1981 (2 ABF), 28 Jan 1982 (47 ABF), 5 Jul 1984 (1 ABF); NEMP Sta. 32, 10 Jul 1984 (1 ABF); NEMP Sta. 39, 12 Jul 1980 (19 ABF).

Description.—Preserved specimens colorless to light tan. Largest complete specimen 37 mm long, 1.5 mm wide, with 136 setigers. Largest fragment 40 mm long, 1.5 mm wide, with 98 setigers. Prostomium (Fig. 5a) short, bluntly conical, only slightly longer than wide. First peristomial segment as long as setiger 1, second somewhat shorter. Setigers wider than long throughout body, body wider anteriorly. Postsetal lobes short throughout; anterior parapodia gently rounded in juveniles, gently rounded or obliquely truncate in adults (Fig. 5b), conical in median (Fig. 5c) and posterior parapodia (Fig. 5d). Presetal lobes low, rounded in anterior parapodia; conical posteriorly. Large specimens with 2 pairs of anal cirri, dorsal pair twice as long as ventral pair; smaller specimens usually with two dorsal anal cirri. Anterior parapodia with 4–5 limbate setae dorsally, followed by 5–9 (3–13) composite hooks, and 0–2 setae; greatest numbers occurring about setiger 6. Composite hooded hooks on first 16 setigers (5–18); blades short in proportion to shaft and of similar length on all setigers; hood at distal end of shaft projecting beyond width of blade. Composite hooks with 7–8 teeth of equal size, main fang only slightly larger than preceding tooth (Fig. 5e). Simple hooded hooks (2–4 per parapodium) starting on setiger 17 (6–19) with 8–9 teeth decreasing apically in size, main fang entire or subdivided in median (Fig. 5f) and posterior setigers (Fig. 5g). Limbate setae lacking after setiger 40. Aciculae yellow, 2 per parapodium in anterior half of body, 1 thereafter; distal tips tapering and blunt in anterior and median parapodia, long and tapering with tips projecting in posterior parapodia.

Mandibles translucent, fused for two thirds of their length (Fig. 5h). Maxillary apparatus medium to dark brown. Maxillary carriers broad, width deeply constricted, permanently divided; M I base broad, tips falcate; M II with 4 teeth of equal size, with large space between distal teeth (Fig. 5i), some small specimens with evenly spaced teeth; M III unidentate with arched cutting edge and basal edge; M IV with long blunt tooth, riding hat-shaped, M V (Fig. 5j) free standing, displaced outward to M IV. Tips of M I and M II usually fit under tooth of M III (Fig. 5j), but in 2 specimens, tip of M II fit under M III, while tip of M I was above tooth of M IV (Fig. 5k).

Remarks.—There are only slight variations between our species and *L. cingulata* from southern oceans. Orensanz (1973:363–364, 1990:82–85) examined numerous specimens (including some types) and considers the following species as synonyms of *L. cingulata*: *L. magalahaensis* sensu Ehlers, 1900 (not Kinberg 1865); *L. virgini* Kinberg, 1865 (in part); *L. patagonica* Hartmann-Schröder, 1962; and *L. limbata* Hartmann-Schröder, 1965. Orensanz (1973) described *L. cingulata* as having 3–6 (usually 4) teeth on M II. His pl. 21, fig. e (1990) shows 4 evenly spaced teeth, while our mature specimens have 4 teeth on M II with a space between the distal teeth. M III of our species is similar to the M III in pl. 22, fig. c (from paratype of *L. patagonica*) and M IV is similar to the M IV in pl. 22, fig. f (from paratype of *L. limbata*). The southern species has composite hooks to setigers 19–21 (15–25), instead of to setiger 16 (5–18). None of the *L. cingulata* examined by Orensanz (pers. comm.) was complete. However, small specimens of the closely related *L. kerguelensis* also had 4 anal cirri with the dorsal pair longer (see Orensanz 1990; pl. 40, fig. c).

Lumbrineris cingulata resembles *L. cruzensis* Hartman, 1944a and *L. latreilli* Audouin & Milne Edwards, 1833. *Lumbrineris cruzensis* has a similarly shaped prostomi-

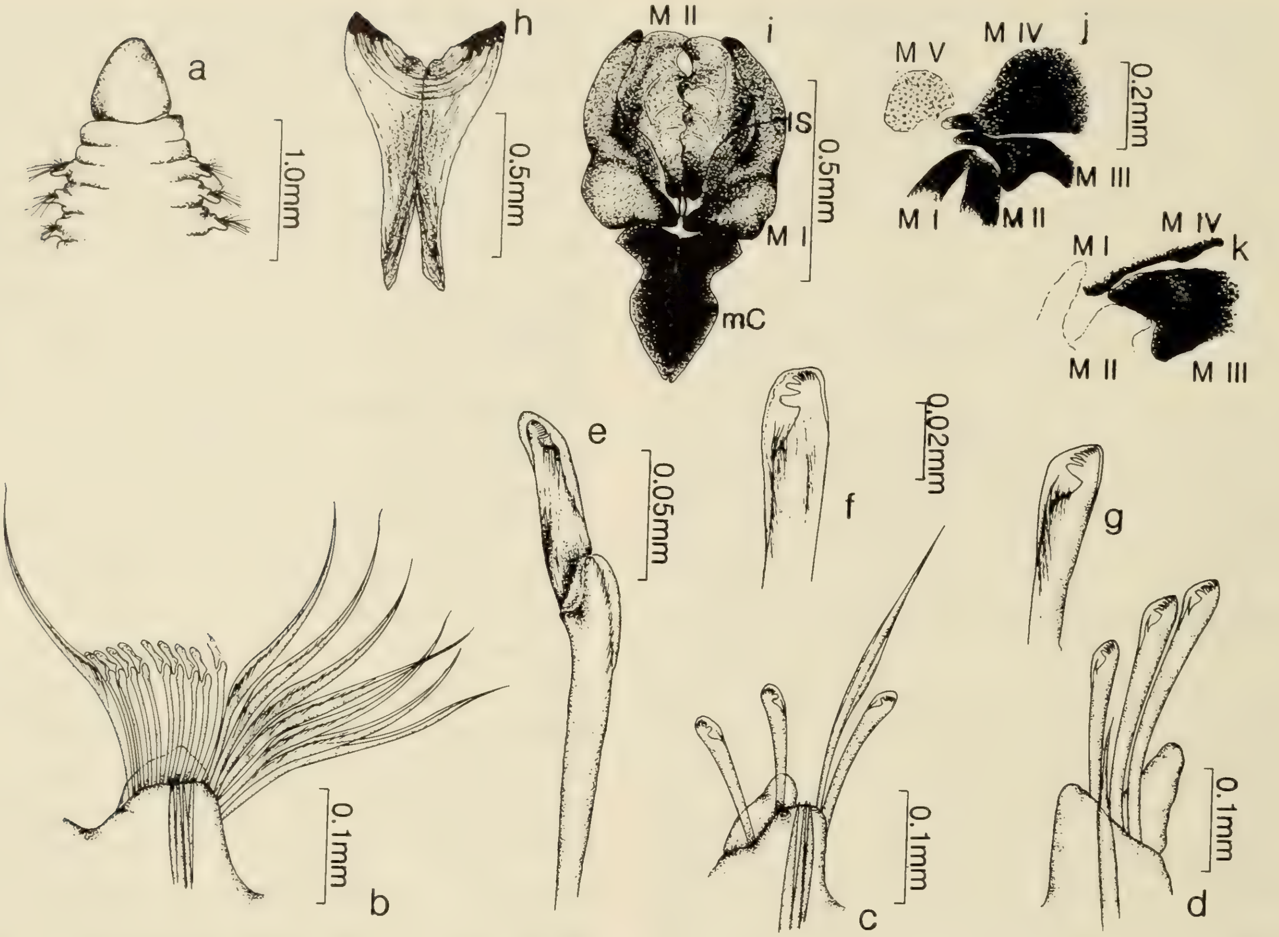

Fig. 5. *Lumbrineris cingulata*: a, Prostomium; b, Left parapodium 6; c, Parapodium 37; d, Posterior parapodium; e, Composite hooded hook from parapodium 6; f, Simple hook from parapodium 27; g, Hook from posterior parapodium; h, Mandibles; i, Maxillary carriers, M I and M II; j, Left M III, M IV and lateral support; k, Left M III.

um, a similar maxillary formula, and setigers 1–16 have short-bladed compound hooks. However, *L. cruzensis*' mandibles are fused for most of their length, and it has a bilabiate parapodium posteriorly. *Lumbrineris latreilli* has 2 teeth on M III instead of 1, and the blades of the composite hooks are longer anteriorly instead of being of equal length throughout.

Distribution.—Northwestern Atlantic specimens: Massachusetts to Virginia; 15–244 m. Grain size range from granular to coarse clay; greatest numbers in fine sand to very fine silt. TOC values from 0.7–17.6 mg/g. Southern ocean specimens: Falkland Islands to La Plata River, Argentina; Tierra del Fuego; Magellan Strait, north to central Chile; Scotia Sea; and Antarctic peninsula; 0–1000 m. Common on sheltered sandy-silt beaches, and shallow subtidal calm waters.

Genus *Paraninoe* Levenstein, 1977

Type species.—*Ninoe fusca* Moore, 1911; designated Levenstein 1977.

Diagnosis.—Prostomium conical, may have a retractable nuchal papilla. Parapodia uniramous, with simple limbate setae and simple, multidentate hooded hooks, blades of hooks long in anterior parapodia. Notopodia reduced; parapodia with a simple digitate branchia. M III and IV unidentate, M V lacking. Aciculae black.

The digitate postsetal lobe combined with the shape of the parapodia is a distinct morphological combination of this genus. The digitate postsetal lobe on anterior setigers is frequently referred to as a single lobe branchia, corresponding to the multilobed branchiae in the genus *Ninoe,* while in the median and posterior setigers it is referred to as a postsetal lobe.

Paraninoe brevipes (McIntosh, 1903)
Fig. 6

Lumbriconeris brevipes McIntosh, 1903:147–149, text fig. 3, pl. 12, figs. 33–34.

Lumbrineris brevipes.—Pettibone, 1963:260–262, fig. 68h.—Fauchald, 1970:217.—Day, 1973:62.—Uebelacker, 1984:Ch. 41, pp. 19–21, figs. 15, 16a–h.

Ninoe brevipes.—Hartman and Fauchald, 1971:85–86, pl. 11, fig. a.

Paraninoe brevipes.—Levenstein, 1977: 191.—Miura, 1980:1046–1048, fig. 13A–C.—Orensanz, 1990:96.

Material examined.—Northwestern Atlantic, Off NE USA: NEMP Sta. 13, 17 Aug 1981 (1 ABF); NEMP Sta. 20, 28 Apr 1978 (4 ABF), 22 Jul 1979 (2 ABF), 19 Sep 1979 (2 ZMUC, 2 ABF), 11 Dec 1979 (1 ABF), 16 Jul 1980 (1 ZMUC), 10 Dec 1980 (1 ABF), 15 Jul 1981 (6 ABF), 2 Feb 1982 (14 ABF), 28 Aug 1982 (3 USNM 146108, 2 ZMUO, 4 ABF), 7 Jul 1983 (8 ABF), 5 Jul 1984 (6 USNM 146109, 10 ABF); NEMP Sta. 22, 11 Jul 1980 (2 ABF); NEMP Sta. 28, 5 Jul 1983 (1 ABF); NEMP Sta. 37, 11 Dec 1983 (4 ABF).

Description.—Preserved specimens colorless, slightly iridescent. Largest fragment 2.2 mm wide. Largest complete specimen 21 mm long, 1.5 mm wide, with 109 setigers. Prostomium conical, longer than wide (Fig. 6a). First peristomial segment longer than second, second equal to first setiger. Anterior postsetal lobes of parapodia 1–2 small, conical; lengthening on setigers 3–5 (Fig. 6b); digitate and directed distally in setigers 6–30; shortening, becoming thumb of mitten-shaped in median (Fig. 6c, d) and posterior parapodia (Fig. 6e). Presetal lobes low, rounded in anterior and median parapodia, thin and conical in posterior ones. Largest complete specimen with 2 anal cirri, juveniles with single lobe.

Anterior parapodia with 3 or 4 limbate setae in superior position, followed by 4 long-bladed hooded hooks and a single inferior seta. All limbate setae with long acute tips, becoming fewer in number after setiger 14, totally lacking after setiger 98 (large specimen). Long slender-bladed hooded hooks (Fig. 6f) starting on setiger 1, replaced by shorter hooks with wider blades (Fig. 6g) on setiger 14 (10–18), posterior hooks bulbous (Fig. 6h). Long-bladed anterior hooks with 6–7 teeth of equal size, median ones with 8–10 teeth of equal size above a main fang occasionally subdivided; posterior hooks with 6–12 fine teeth above a main fang usually subdivided into 2–4 teeth. Limbate setae and long slender hooks with blades pale yellow, shafts a darker color; shorter hooks all gold or gold with shafts a deep gold. Aciculae deep gold, dark brown or black, 2–3 per parapodium with filamentous tips projecting through parapodial wall; distal part deep gold. Hooks and aciculae a lighter color in anterior setigers, darker in posterior ones. Hooks and aciculae of lighter color in juveniles than in adults. Vascular loops frequently discernable in some median postsetal lobes in specimens 1.5 mm wide or larger, preserved for months or years.

Mandibles (Fig. 6i) white, well calcified with blades close together but not fused. Maxillary apparatus (Fig. 6j) medium brown, hard. Maxillary carriers long, broad, slightly constricted medially; M I base broad, tips falcate; M II with 3 evenly spaced teeth; M III with long blunt tooth; M IV riding-hat shaped, M V lacking except for a single specimen with large unattached, nearly circular M V.

Remarks.—In addition to *P. brevipes,* the genus *Paraninoe* includes the following species:

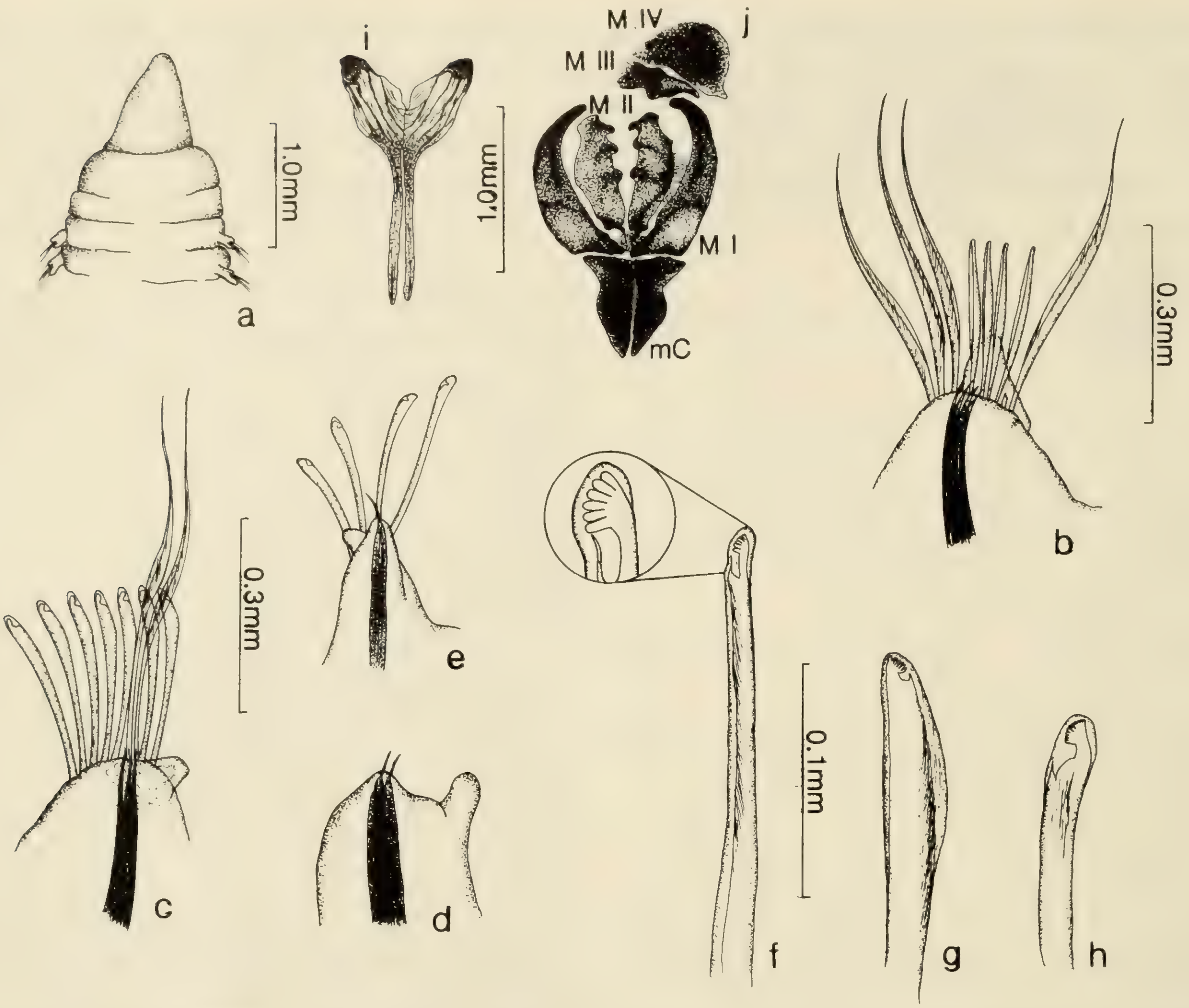

Fig. 6. *Paraninoe brevipes*: a, Prostomium; b, Right parapodium 5; c, Parapodium 40; d, Median parapodium, side view; e, Posterior parapodium; f, Hooded hook from parapodium 4; g, Hook from parapodium 27; h, Hook from posterior parapodium; i, Mandibles; j, Maxillae.

Lumbrineris abyssalis Imajima & Higuchi, 1975; Japan; 590–1055 m.
Lumbrineris antarctica Monro, 1930; Antarctica; 365–3747 m.
Ninoe fusca Moore, 1911; California, and Kermadec Trench; 2770–7000 m.
Ninoe fuscoides Fauchald, 1972; California; 2230–2650 m.
Paraninoe hartmanae Levenstein, 1977; Alaska, Kuril-Kamchatka and Japanese Trenches; 6157–8100 m.
Lumbriconereis minuta Théel, 1879; Arctic.
Augeneria monotentaculata Averincev, 1972; Antarctic.
Lumbrineris nagae Gallardo, 1968; Nha Trang, South Viet Nam.
Ninoe simpla Moore, 1905; Alaska; 238–419 m.

Orensanz (1990:96) considers *P. monotentaculata,* from the same area, to be a synonym of *P. antarctica. Paraninoe fusca* M II has 2 teeth, and the hooks start about setiger 40. *Paraninoe brevipes* and *P. antarctica* M III has 3 teeth, but *P. antarctica* has transitional hooks on setiger 1, while *P. brevipes* hooks and their teeth are clearly defined on setiger 1. *Paraninoe hartmanae, P. fuscoides,* and *P. minuta* M II has 4 teeth; *P. hartmanae* has a large retractable nuchal papilla at the boundary of the prostomium and peristomium, and the hooks start about setiger 100; *P. fuscoides* lacks a nuchal papilla, the hooks start on setiger 1, and the branchiae are located posteroventrally; *P. minuta* lacks a nuchal papilla, the hooks start on setiger 1, and the branchiae are located dorsolaterally (the norm). *Paraninoe simpla* M II has 5–6 teeth, and a nuchal papilla. *Paraninoe abyssalis* and *P. nagae* M II has 7 teeth. Both have a nuchal papilla, but *P. abyssalis* hooks start on setiger 1, while *P. nagae* hooks start from setiger 60–100.

The genus *Paraninoe* differs from *Ninoe* in that it lacks multilobed branchiae, and M III and M IV have smooth cutting edges instead of denticulations on one or both maxillae. *Paraninoe brevipes* differs from *N. nigripes* Verrill, 1873 in the shape of M IV, being riding-hat shaped in the former and irregular-shaped in the latter, and in the length of the anterior postsetal lobe, with it being equal to or less than its parapodium in *P. brevipes* and exceeding it in *N. nigripes.* As the juveniles of *N. nigripes* lack branchiae until they are 0.4–0.6 mm wide, it is the length of the postsetal lobe (setigers 3–13) that is used to separate juveniles of the two species. Both species have in common: limbate setae with long acute tips; long-bladed hooks starting on setiger 1; setae dark at their base with blades lighter; black aciculae; similar shaped parapodia including the mitten-shaped ones in median and posterior setigers; and 0–2 anal cirri.

Uebelacker (1984:Ch. 41, p. 21) noted that her specimens of *P. brevipes* have a "small, globular nuchal papilla located middorsally at the base of prostomium, concealed by anterior margin of peristomium." The nuchal papilla was not discernable in our specimens.

Distribution.—Massachusetts to North Carolina, Gulf of Mexico, southern California, northwestern Spain; 65–6684 m. Grain size range from very fine sand to fine silt; greatest numbers in fine silt to coarse silt. TOC values from 3.0–20.5 mg/g.

Scoletoma Blainville, 1828, emended

Type species.—*Lumbricus fragilis* O. F. Müller, 1776; designated by Blainville, 1828.

Diagnosis.—Prostomium conical or globular, usually without papillae, occasionally with a singular papilla in nuchal fold. Parapodia uniramous, or with notopodial rudiments. Parapodia with simple limbate setae and simple, multidentate hooded hooks. M V free standing and displaced outward to M IV. Aciculae yellow or black, of lighter color in juveniles.

According to the literature the following species of *Scoletoma* are present in the northwestern Atlantic in addition to the ones found in this study: *S. atlantica* (sensu Hartman, 1965); *S. ernesti* (Perkins, 1979); *S. impatiens* (Claparède, 1868); *S. punctata* (McIntosh, 1885); and *S. verrilli* (Perkins, 1979).

Key to the Northwestern Atlantic species of *Scoletoma*

1. Maxillae III unidentate 2
– Maxillae III bidentate 6
2. Aciculae yellow 3
– Aciculae black .... *S. fragilis*
3. Hooks starting on setiger 1 4
– Hooks starting after setiger 1 5
4. Maxillae IV riding hat-shaped, 0–4 anal cirri .... *S. hebes*
– Maxillae IV gum drop-shaped, 0–2 anal cirri .... *S. verrilli*
5. Posterior parapodia with short postsetal lobes ....
.... *S. atlantica* sensu Hartman, 1965
– Posterior parapodia with long postsetal lobes .... *S. tenuis*
6. Aciculae yellow 7
– Aciculae black .... *S. acicularum*
7. Hooks starting on setiger 1 ......
.... *S. impatiens*
– Hooks starting after setiger 1 8
8. Prostomium long, acutely conical; with long medium setae .. *S. punctata*

– Prostomium short, subconical; without long median setae .. *S. ernesti*

Scoletoma acicularum (Webster & Benedict, 1887), new combination

Fig. 7

Lumbrinereis acicularum Webster & Benedict, 1887:725, pl. 4, figs. 55–59.
Lumbrineris acicularum.—Fauchald, 1970: 87, 218.
Lumbrineris fragilis.—Pettibone, 1963:262, fig. 69a–j.—Hartman & Fauchald, 1971: 82–83.—Day, 1973:62.—Gardiner, 1976: 197–198. (Not O. F. Müller, 1776.)

Material examined.—Northwestern Atlantic, Off NE U.S.A.: NEMP Sta. 2, 20 Jul 1980 (4), 31 Aug 1982 (1), 10 Jul 1983 (1), 12 Jul 1984 (1); NEMP Sta. 3, 14 Dec 1979 (1), 20 Jul 1980 (1), 6 Dec 1980 (3), 11 Jul 1981 (2), 10 Jul 1983 (2), 13 Jul 1984 (3); NEMP Sta. 7, 19 Apr 1978 (9), 24 Apr 1979 (10), 15 Dec 1979 (5), 20 Jul 1980 (5), 7 Dec 1980 (14), 12 Jul 1981 (4 ABF, 15), 8 Feb 1982 (6), 31 Aug 1982 (1); NEMP Sta. 8, 15 Dec 1979 (2 ABF, 4), 20 Jul 1980 (20), 7 Dec 1980 (2 ABF, 28), 12 Jul 1981 (6), 8 Feb 1982 (23), 30 Aug 1982 (3 ABF, 75), 10 Jul 1983 (109); NEMP Sta. 9, 19 Jul 1980 (62), 8 Dec 1980 (15), 13 Jul 1981 (10 ABF, 53), 9 Feb 1982 (38), 30 Aug 1982 (80), 9 Jul 1983 (8); NEMP Sta. 10, 21 Apr 1978 (1), 26 Apr 1979 (12); NEMP Sta. 11, 21 Apr 1978 (2, USNM 146110, 4 ABF), 21 Sep 1978 (2), 23 Apr 1979 (1), 26 Sep 1979 (2), 16 Dec 1979 (1 ABF, 2), 19 Jul 1980 (5), 8 Dec 1980 (1), 13 Jul 1980 (6), 9 Feb 1982 (11), 29 Aug 1982 (11), 9 Jul 1983 (12), 10 Jul 1984 (12); NEMP Sta. 12, 16 Dec 1978 (5 ZMUO, 1 ABF), 18 Jul 1980 (2), 9 Dec 1980 (9), 13 Jul 1981 (5), 9 Feb 1982 (19), 29 Aug 1982 (20), 9 Jul 1983 (13); NEMP Sta. 13, 22 Apr 1978 (6), 20 Sep 1978 (1), 22 Apr 1979 (5 ZMUC), 13 Sep 1979 (1), 17 Dec 1979 (3), 22 Jul 1980 (9), 9 Dec 1980 (9), 17 Aug 1981 (2), 10 Feb 1982 (13), 29 Aug 1982 (12), 9 Jul 1984 (10); NEMP Sta. 14, 19 Jul 1979 (2); NEMP Sta. 17, 26 Apr 1978 (3 USNM 146111, 4 ZMUC, 4 ZMUO, 7 ABF), 24 Sep 1978 (73), 21 Apr 1979 (40), 20 Jul 1979 (42), 22 Sep 1979 (32), 13 Dec 1979 (37), 2 Aug 1980 (41), 5 Dec 1980 (32), 14 Aug 1981 (50), 6 Feb 1982 (13), 14 Sep 1982 (11), 12 Jul 1983 (3 ABF, 31), 27 Aug 1984 (1 ABF), 17 Jun 1985 (3 ABF, 21); NEMP Sta. 18, 6 Jul 1984 (1); NEMP Sta. 20, 27 Sep 1978 (2), 11 Dec 1979 (1), 16 Jul 1980 (2), 28 Aug 1982 (12); NEMP Sta. 22, 11 Jul 1980 (1), 31 Jan 1982 (1); NEMP Sta. 23, 1 May 1978 (1), 29 Sep 1978 (1), 25 Jul 1979 (1 ABF), 17 Sep 1979 (2), 12 Jul 1980 (2), 18 Dec 1980 (2), 18 Jul 1981 (1 ABF), 31 Jan 1982 (1), 27 Aug 1982 (1 ABF, 4); NEMP Sta. 24, 30 Sep 1978 (4), 12 Jul 1980 (3); NEMP Sta. 25, 2 May 1978 (5 ABF); NEMP Sta. 26, 2 May 1978 (1); NEMP Sta. 28, 17 Dec 1980 (1), 20 Jul 1981 (1); NEMP Sta. 31, 21 Jul 1980 (14), 11 Jul 1983 (1), 10 Jul 1984 (1); NEMP Sta. 32, 21 Jul 1980 (2), 6 Dec 1980 (7), 11 Jul 1983 (1 ABF, 7), 10 Jul 1984 (8 ABF, 19), 18 Jun 1985 (5 ABF, 11); NEMP Sta. 33, 13 Dec 1979 (1), 1 Aug 1980 (1), 13 Aug 1981 (2), 6 Feb 1982 (4), 16 Jun 1985 (1 ABF); NEMP Sta. 36, 14 Jul 1980 (6), 2 Dec 1980 (3), 22 Jul 1981 (1 ABF), 26 Jan 1982 (1), 15 Sep 1982 (3), 1 Jul 1983 (2 ABF, 4), 2 Jul 1984 (2), 22 Jun 1985 (2 USMN 146112, 1 ZMUC, 4 ZMUO, 6 ABF); NEMP Sta. 37, 11 Dec 1980 (1), 28 Aug 1982 (1); NEMP Sta. 39, 12 Jul 1980 (2); NEMP Sta. 15A, 5 Oct 1978 (14), 20 Apr 1979 (7), 18 Jul 1979 (4), 21 Sep 1979 (1), 2 Sep 1982 (5), 13 Jul 1983 (5), 31 Aug 1984 (15), 14 Jun 1985 (10 ABF, 8); NEMP Sta. 16A, 24 Apr 1978 (2), 25 Sep 1978 (1), 20 Apr 1979 (1), 19 Jul 1979 (7), 12 Dec 1979 (1), 30 Jul 1980 (6), 5 Feb 1982 (2), 9 Sep 1982 (1), 13 Jul 1983 (2); NEMP Sta. 16C, 19 Jul 1979 (1), 12 Dec 1979 (6), 31 Jul 1980 (9), 5 Dec 1980 (6), 13 Jul 1983 (15), 29 Aug 1984 (3), 15 Jun

1985 (6); NYB Sta. 2, 28 Jul 1980 (1 ABF); NYB Sta. 4, 2 Oct 1985 (8); NYB Sta. 7, 1 Oct 1985 (1); NYB Sta. 8, 15 Aug 1981 (6), 10 Sep 1982 (1), 23 Aug 1984 (5), 2 Oct 1985 (1); NYB Sta. 10, 15 Aug 1981 (1); NYB Sta. 11, 12 Aug 1981 (1), 12 Sep 1982 (4), 25 Aug 1894 (5), 2 Oct 1985 (4); NYB Sta. 12, 12 Aug 1981 (2), 13 Sep 1982 (8), 21 Jul 1983 (4), 25 Aug 1984 (2), 2 Oct 1985 (7); NYB Sta. 13, 31 Jul 1980 (3); NYB Sta. 14, 1 Aug 1980 (7), 13 Aug 1981 (3), 5 Sep 1983 (7), 28 Aug 1984 (1), 3 Oct 1985 (7); NYB Sta. 16, 30 Aug 1984 (2); NYB Sta. 17, 1 Aug 1980 (5), 5 Sep 1983 (1), 30 Aug 1984 (1); NYB Sta. 19, 3 Jul 1980 (1), 12 Sep 1982 (1), 21 Jul 1983 (1), 31 Aug 1984 (1); NYB Sta. 20, 30 Jul 1980 (5 ABF), 11 Sep 1982 (9), 19 Jul 1983 (7), 31 Aug 1984 (3), 30 Sep 1985 (2); NYB Sta. 21, 11 Sep 1982 (1), 20 Jul 1983 (2), 31 Aug 1984 (1), 30 Sep 1985 (1); NYB Sta. 22, 30 Jul 1980 (8), 11 Aug 1981 (1), 9 Sep 1982 (7), 5 Jul 1983 (8), 1 Oct 1985 (6); NYB Sta. 23, 14 Aug 1981 (2), 27 Aug 1984 (3); NYB Sta. 24, 20 Jul 1983 (8), 27 Aug 1984 (5), 4 Oct 1985 (5); NYB Sta. 25, 3 Aug 1980 (5), 20 Jul 1983 (7), 6 Sep 1983 (1), 4 Oct 1985 (1); NYB Sta. 26, 4 Oct 1985 (2); NYB Sta. 27, 3 Aug 1980 (7), 14 Aug 1981 (3), 14 Sep 1982 (2), 27 Aug 1984 (6 ABF), 4 Oct 1985 (5); NYB Sta. 28, 2 Aug 1980 (4), 13 Aug 1981 (4), 6 Sep 1983 (3), 28 Aug 1984 (2 ABF, 5), 3 Oct 1985 (1); NYB Sta. 29, 30 Jul 1980 (1), 31 Aug 1984 (3); NYB Sta. 30, 30 Jul 1980 (3), 12 Aug 1981 (3), 9 Sep 1982 (5), 6 Sep 1983 (9), 31 Aug 1984 (1 ABF, 3), 3 Oct 1985 (2); NYB Sta. 31, 1 Oct 1985 (2); NYB Sta. 32, 29 Jul 1980 (1), 15 Sep 1982 (2), 31 Aug 1984 (5), 1 Oct 1985 (6); NYB Sta. 33, 15 Sep 1982 (6), 30 Aug 1984 (7), 30 Sep 1985 (2 ABF); NYB Sta. 35, 9 Sep 1982 (1), 21 Jul 1983 (1), 30 Aug 1984 (2), 1 Oct 1985 (2); NYB Sta. 36, 1 Aug 1980 (1), 11 Aug 1981 (2), 6 Sep 1983 (2), 30 Aug 1984 (1), 3 Oct 1985 (1); NYB Sta. 37, 1 Aug 1980 (1), 11 Oct 1985 (1); NYB Sta. 38, 1 Aug 1980 (1), 11 Aug 1981 (4), 6 Sep 1983 (1), 3 Oct 1985 (2); NYB Sta. 39, 29 Jul 1980 (1), 12 Aug 1981 (2), 9 Sep 1982 (2), 6 Sep 1983 (1), 30 Aug 1984 (2), 3 Oct 1985 (4); NYB Sta. 40, 31 Jul 1980 (2), 9 Sep 1982 (5), 1 Oct 1985 (2); NYB Sta. 41, 4 Aug 1980 (2); NYB Sta. 42, 13 Sep 1982 (2), 20 Jul 1983 (2), 31 Aug 1984 (2), 2 Oct 1985 (8); NYB Sta. 43, 31 Aug 1984 (2 ZMUC, 3 ABF), 2 Oct 1985 (3); NYB Sta. 44, 15 Aug 1981 (9), 31 Aug 1984 (1 USNM 146113, 3 ABF), 2 Oct 1985 (4); NYB Sta. 63, 19 Aug 1981 (1), 7 Sep 1983 (2), 31 Aug 1984 (5), 30 Sep 1985 (3), NYB Sta. 64, 30 Sep 1985 (1); NYB Sta. 65, 19 Jul 1983 (8), 31 Aug 1984 (6), 30 Sep 1985 (1); NYB Sta. 158, 16 Aug 1981 (2), 5 Sep 1983 (2), 28 Aug 1984 (3), 3 Oct 1985 (1).—Massachusetts, Marblehead Harbor: 4 Apr 1954 (16), M. Pettibone ID as *Lumbrineris fragilis* (USNM 30097).

Description.—Preserved material colorless to salmon color, iridescent. Largest specimen (incomplete) 156 mm long, 4.5 mm wide, with 273 segments. Prostomium short, bluntly conical, basal width and length about equal (Fig. 7a). First peristomial segment longer than second, equal in width to first setiger. Body uniform in width to median region, then tapering gradually towards posterior end. Postsetal lobes of anterior parapodia (Fig. 7b) short, roughly conical or truncate, narrowing in median segments (Fig. 7c), becoming more digitate and longer in posterior parapodia (Fig. 7d). Postsetal lobes of posterior parapodia about a third longer than those of anterior parapodia. Presetal lobes low, rounded, wider than postsetal lobes throughout. Mature specimens with 4 anal cirri of equal size, juveniles usually with 2 anal cirri or a single lobe (Table 3).

Anterior parapodia with up to 18 limbate setae, most numerous on setigers 6–9, superior setae longer than inferior setae; setae less numerous through median region, usually lacking after setigers 60–70. Simple hooded hooks with 8–9 teeth beginning on

Table 3.—*Lumbrineris acicularum*: relationship of pygidium appendages to size.

Width in mm	0.09–0.13*	0.20–0.24**	0.25–0.29	0.30–0.39	0.4–0.49	0.5–0.59	0.6–0.69	0.7–0.79***	0.8–0.89	0.9–2.3
Single lobe	2	3	3							
2 anal cirri				4	5	5	1	1		
4 anal cirri									1	6

* Specimen: 0.4 mm by 0.9 mm; with 6 segments, 5 setigers; setiger 1 with 1 limbate seta; pygidium with single lobe.

** Specimen: 1.15 mm by 0.2 mm; with 10 setigers; setiger 1 with 1 limbate seta and 1 bulbous hooded hook; pygidium with single lobe.

*** Specimen: 10 mm by 7.2 mm; with 52 setigers; setiger 1 with 4 limbate setae; setiger 5 with slender-bladed hooded hook (first occurrence) and 4 limbate setae; pygidium with 2 anal cirri.

setigers 35–40 in mature specimens (Fig. 7e), may be preceded on 1–2 setigers by a single hook with slightly longer blade. Teeth of hooded hooks decreasing in size apically above a subdivided main fang. Posterior hooks with 4–6 teeth above whole or subdivided main fang (Fig. 7f, g). In juveniles 5 mm long by 0.65 mm wide, hooks beginning on setiger 1; 12 mm by 1 mm, hooks beginning about setiger 6; hooks beginning further back with increasing size. Limbate setae and hooded hooks yellow. Aciculae black or dark brown basally, tips usually deep gold; color darker posteriorly in adults. Aciculae color gold to deep gold in juveniles, color darkest in median region. Aciculae numbering 3–5 in anterior, 1 in posterior parapodia. Faint poorly defined vascular loops discernable in some large specimens.

Mandibles hard, fused for half their length; upper edge flat in small adults 2 mm wide, with added calcareous plate in those of 4 mm (Fig. 7h). Maxillary apparatus deep brown, hard with calcified cutting edges. Maxillary carriers long, incised anteriorly in 2 mm wide specimens (Fig. 7i); incised at junction with M I in 4 mm wide specimens, much shorter in proportion to M I and usually folded together (Fig. 7j). M I falcate; M II usually with 4 sawlike teeth, smaller 5th tooth present between distal teeth in about 10% of specimens; M III bidentate (Fig. 7k); M IV unidentate, only slightly larger than M III. M V free standing, displaced out to M IV, roughly oval.

Remarks.—The original description by Webster & Benedict (1887) is brief and incomplete. The color of aciculae or maxillary formula is not mentioned. However, in pl. 4, fig. 55 of the maxillary apparatus, M III appears bidentate on right side and unidentate on left. The first complete description of *S. acicularum* is given in Moore's unpublished manuscript, circa 1900. Moore briefly noted that *S. fragilis* (O. F. Müller, 1776) has a single tooth on M III, a large wing plate on M IV, and that Verrill (1873) had found it in the Woods Hole region, in the deeper waters off Vineyard Sound.

Scoletoma acicularum can be distinguished from *S. fragilis* in that *S. acicularum* has: two teeth instead of one on M III; a smaller and irregular-shaped M IV instead of the riding-hat shaped one; roughly conical postsetal lobes on anterior parapodia instead of the wide, flaplike or ear-shaped ones; slightly longer postsetal lobes in posterior parapodia; and 4 anal cirri in mature specimens instead of two. *Scoletoma fragilis* also has long capillary setae in the median parapodia, notopodial rudiments present on the presetal lobes to mid-body, and hook(s) present between the superior and inferior setae on numerous setigers in medium-size specimens.

Juveniles of *S. acicularum* and *S. fragilis* can be confused with juveniles of *Paraninoe*

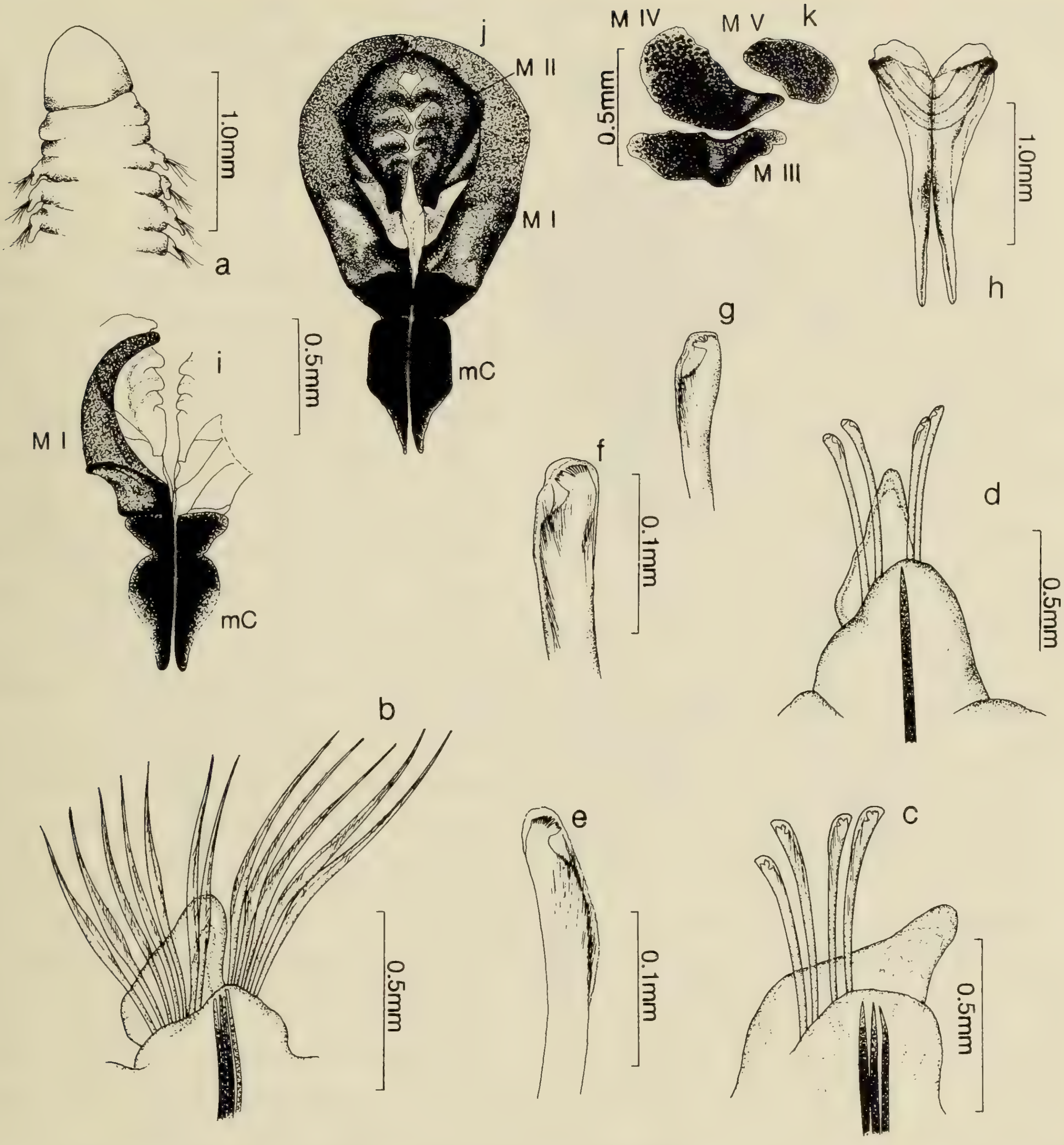

Fig. 7. *Scoletoma acicularum*: a, Prostomium; b, Right parapodium 4; c, Parapodium 83; d, Posterior parapodium from juvenile; e, Hooded hook from setiger 67; f, Hook from posterior parapodium from 4 mm specimen; g, Hook from posterior parapodium of juvenile; h, Mandibles; i, Maxillary carriers, M I and M II from 2 mm specimen; j, Maxillary carriers, M I and M II from 4 mm specimen; k, Right M III, M IV and MV from 4 mm specimen.

brevipes (McIntosh, 1885) and *Ninoe nigripes* Verrill, 1873 (*N. nigripes* lacks branchiae until it is 0.4–0.6 mm wide). However, the anterior postsetal lobes of *S. acicularum* and *S. fragilis* are of different shape than the digitate lobes of *P. brevipes* and *N. nigripes.*

Distribution.—Nova Scotia to North Carolina; low water–244 m. Grain size range from granular to coarse clay; greatest numbers in very coarse sand to medium sand. TOC values from 0.3–24.0 mg/g. Most abundant at stations with TOC values less than 4 mg/g, usually absent from stations with high organic content.

Scoletoma fragilis (O. F. Müller, 1776)
Fig. 8

Lumbricus fragilis O. F. Müller, 1776:216; 1779:45, figs. 1–3; 1781:83.
Scoletoma fragilis.—Blainville, 1828:492.
Lumbrinereis fragilis.—Verrill, 1881:297, 299, 301, 304, 308, 311, 316.—Webster & Benedict, 1887:725.
Lumbriconereis fragilis.—McIntosh, 1903: 158.—Fauvel, 1923:430, fig. 171k, l.—Wesenberg-Lund, 1950a:27; 1950b:69–70, charts 19, VIII, d, H; 1951:55–56, chart 28; 1953:51.—Ushakov, 1955:242 (not McIntosh, 1910:372–376, pl. 62, fig. 1–1a, pl. 73, fig. 8–8c, pl. 82, fig. 2–2b).
Lumbrineris fragilis.—Hartman, 1944a: 139.—Fauchald, 1970:217.—Hartmann-Schröder, 1971:255, fig. 85a–g.—Campoy, 1982:611–612.—George & Hartmann-Schröder, 1985:128–129, fig. 40a–e (not Pettibone, 1963:262, fig. 69.—Hartman & Fauchald, 1971:82–83.—Day, 1973:62.—Gardiner, 1976:197–198).

Material examined.—Northwestern Atlantic, Off NE USA: NEMP Sta. 13, 17 Dec 1979 (1 USNM 146114); NEMP Sta. 19, 10 Dec 1979 (2 ZMUC, 2 ABF), 15 Jul 1980 (1 USNM 146115), 10 Dec 1980 (5 ABF), 15 Jul 1981 (2), 2 Sep 1982 (2 ZMUC), 5 Jul 1984 (2 ZMUC, 2 ZMUO, 3 ABF); NEMP Sta. 20, 11 Dec 1979 (1 ABF); NEMP Sta. 28, 4 Dec 1979 (1 ABF), 17 Dec 1980 (1 USNM 146116, 1 ABF), 28 Jan 1982 (1 ABF); NEMP Sta. 35, 4 Dec 1979 (12 ABF), 14 Jul 1980 (3 USNM 146117, 1 ZMUO), 15 Dec 1980 (5 ABF), 21 Jul 1981 (22 ABF), 29 Jan 1982 (7 ABF), 16 Sep 1982 (18 ABF), 3 Jul 1984 (3 ZMUC, 3 ABF), 25 Jun 1985 (1 ABF); NEMP Sta. 37, 28 Aug 1982 (3 ABF), 27 Jan 1983 (2 ZMUC, 2 ABF), 5 Jul 1984 (5 USNM 146118); NYB Sta. 21, 28 Jul 1980 (1 ABF).—Gulf of Maine: EPA Sta. 8, 42°20.75′N, 70°39.24′W, 21 Sep 1990, 36 m, B. Dinkins ID.

Description.—Preserved material colorless, tan or salmon color, slightly iridescent. Largest specimen (incomplete) 120 mm long, 4.3 mm wide, with 273 segments. Body tapering posteriorly, posterior segments about ⅔ width of anterior ones; segment lengths similar throughout. Prostomium (Fig. 8a) short, bluntly conical, about as long as wide. First peristomial segment equal in length to setiger 1, second segment slightly shorter. Anterior postsetal lobes short, obliquely truncate, flaplike, or ear-shaped (Fig. 8b); conical, reduced in width and height medially (Fig. 8c); conical in posterior parapodia, with height about equal to those of anterior (Fig. 8d). In juveniles (less than 1 mm wide) anterior postsetal lobes rounder, narrower and flaplike. Presetal lobes round, with notopodial rudiment to mid-body. Specimens 2 mm wide with 2 anal cirri; juveniles and smaller specimens with 2 anal cirri or a single lobe.

Superior limbate setae of anterior parapodia longer than inferior setae. Number of limbate setae per fascicle increases from 9 on setiger 1, to 11 on setiger 4, and 14 on setiger 8; thereafter decreasing, none after setigers 25–32. In specimens of 1.5 mm or more wide, longer limbate setae present on setigers 20–40 (18–79) with long, slender blades and whiplike tips (Fig. 8e). Short bulbous hooded hooks beginning on setigers 26–35 in specimens 2–4 mm wide; beginning on setiger 1 in specimen 0.2 mm wide. Hook(s) with longer slender blade (Fig. 8f) between the superior and inferior setae (Fig. 8g), present on specimens of 0.6–3 mm wide, absent in specimens wider than 3 mm, starting as a single hook, numbering 1–3 (rarely 4) per fascicle. Specimen 2.2 mm wide with 1 long hooded hook on setiger 13, 1 on 14, 3 on 15, 2 on 16–19, and 1 on 20; specimens 0.75 mm wide usually with single long hooded hook per parapodium. Each hook with 6–8 teeth decreasing apically in size; main fang occasionally entire in median parapodia (Fig. 8h), otherwise subdivided (Fig. 8i). Mature specimens with 2–3 (rarely

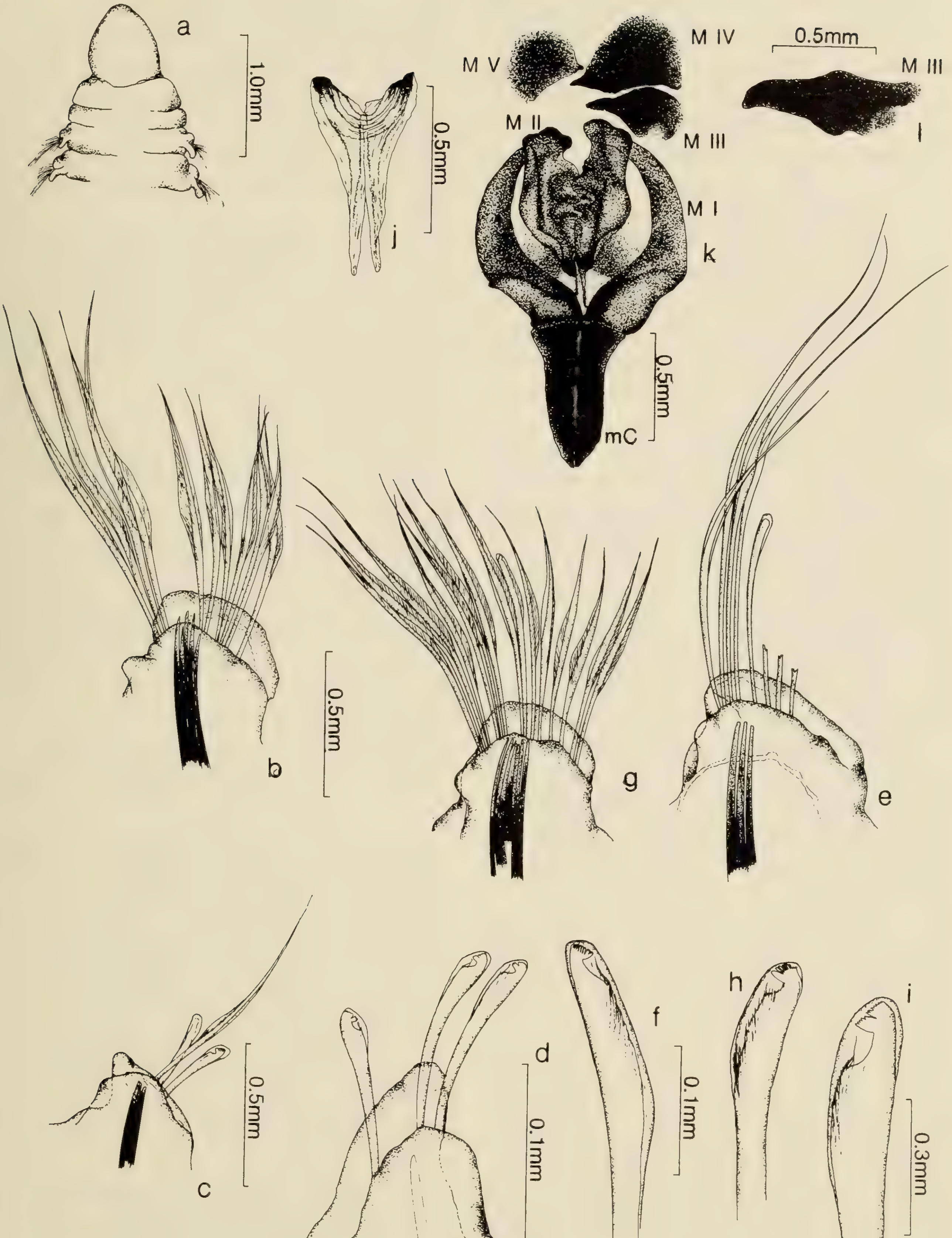

Fig. 8. *Scoletoma fragilis*: a, Prostomium; b, Right parapodium 6; c, Parapodium 94; d, Posterior parapodium from juvenile; e, Parapodium 35, inferior hooks broken; f, Hooded hook from parapodium 9; g, Parapodium 9; h, Hook from parapodium 65; i, Hook from posterior parapodium of juvenile; j, Mandibles; k, Maxillae; l, M III.

4) hooks per fascicle in median parapodia and 3–5 in posterior ones. In anterior parapodia basal tips of limbate setae and hooks usually yellow with shafts a deeper shade of gold; in median parapodia shafts dark gold; and in posterior parapodia blades as well as shafts dark gold, setae absent. Aciculae dark brown, distal tips and sometimes basal tips light gold. Juveniles 0.65 mm wide, hooks and limbate setae yellow throughout, aciculae deep gold in anterior parapodia and beginning of middle ones, yellow (Fig. 8d) in more posterior ones. Vascular loops visible in some presetal lobes as well as in postsetal lobes of large specimens.

Mandibles (Fig. 8j) hard, fused for half their length. Maxillary apparatus (Fig. 8k) dark brown. Maxillary carriers long and broad, slightly constricted medially. M I with broad base and falcate tips; M II with 4 teeth, wide gap between distal teeth, distal tooth largest; M III with long, blunt tooth (Fig. 8l); M IV riding hat-shaped, much larger than M III; M V free standing, displaced outward to M IV.

Remarks.—Hartman (1959:334) noted that the type locality for *S. fragilis* is Denmark. However, according to Dr. Mary E. Petersen, Zoological Museum, University of Copenhagen (pers. comm.), O. F. Müller clearly indicates in later writings (1779:45, 1781:83) that the type locality was near Drobak, on the Oslofjord, where the animal lived in blue clay. She also noted that there are no extant polychaete types of O. F. Müller.

Dr. Inger M. Winsnes (1980) of the Zoological Museum, University of Oslo, collected specimens of *S. fragilis* from the vicinity of Drøbak. Comparisons were made between 5 specimens from Drøbak, Norway, 1 from Lodingen, Lofoten, Norway and 13 from our surveys. Examined were the setigers with short slender hooks and long slender setae, the setigers on which the bulbous hooded hooks began and the shape of the parapodia. The Drøbak specimens and ours were alike, having similar shaped parapodial lobes with notopodial rudiments; similar limbate setae, including the long, slender setae from median parapodia; similar hooded hooks, including the hooks with the slender blades present in specimens of 0.6–3.0 mm wide; similar maxillary apparatus; and a maximum of 2 anal cirri. However, the specimen from Lodingen had a much longer slender hook (similar in appearance to the anterior hook of *S. hebes*) on setiger 20 in the inferior setae bundle, instead of the shorter, slender blade between the two setal groups.

Distribution.—The species described herein has been found from Maine to New Jersey; *S. fragilis* has been reported from Nova Scotia, Iceland, Greenland, Norway, Sweden, Denmark, North Pacific, Mediterranean and English Channel; 21–4250 m. Grain size range in our survey from medium sand to coarse clay; greatest numbers in medium silt to fine sand. TOC values from 0.6–17.0 mg/g.

Scoletoma hebes (Verrill, 1879), new combination
Figs. 9, 10

Lumbriconereis obtusa Verrill, 1874:383; 1875:39 (not Kinberg, 1865).

Lumbrinereis hebes Verrill, 1879:174.

Lumbrineris hebes.—Webster & Benedict, 1887:725.—Moore, 1900:470–472, figs. 45–46; 1909:138.—Pettibone, 1963:264 (in part, not *Lumbriconereis tenuis* Verrill, 1873), fig. 70g–j.—Perkins, 1979:436–439, figs. 8, 9a–c.

Lumbrineris near *tenuis.*—Hartman & Fauchald, 1971:83–84.

Material examined.—Northwestern Atlantic, Off NE USA: NEMP Sta. 2, 14 Dec 1979 (4), 20 Jul 1980 (9); NEMP Sta. 8, 28 Apr 1978 (31), 15 Dec 1979 (25 ABF, 82), 20 Jul 1980 (19), 7 Dec 1980 (22), 12 Jul 1981 (208), 8 Feb 1982 (14), 30 Aug 1982 (18), 10 Jul 1983 (15); NEMP Sta. 9, 19 Jul

1980 (363), 8 Dec 1980 (699), 13 Jul 1981 (113 ABF, 433), 9 Feb 1982 (460), 30 Aug 1982 (158), 9 Jul 1983 (411), 25 Aug 1984 (99 ABF, 100); NEMP Sta. 10, 26 Apr 1979 (1); NEMP Sta. 11, 21 Apr 1978 (60), 21 Sep 1978 (32), 23 Apr 1979 (13), 20 Jul 1979 (8), 26 Sep 1979 (19), 16 Dec 1979 (457), 19 Jul 1980 (28), 8 Dec 1980 (43), 13 Jul 1981 (15), 9 Feb 1982 (100), 29 Aug 1982 (67), 9 Jul 1983 (153), 10 Jul 1984 (178); NEMP Sta. 12, 16 Dec 1979 (18 ZMUO, 5 ABF, 233), 18 Jul 1980 (667), 9 Dec 1980 (320), 13 Jul 1981 (191), 9 Feb 1982 (526), 29 Aug 1982 (471), 9 Jul 1983 (613); NEMP Sta. 13, 22 Apr 1978 (191), 20 Sep 1978 (77), 22 Apr 1979 (115), 13 Sep 1979 (40 USNM 146119, 11 ZMUO, 27 ABF), 17 Dec 1979 (746), 22 Jul 1980 (266), 9 Dec 1980 (55 ABF, 260), 17 Aug 1981 (56 ABF, 148), 10 Feb 1982 (237), 29 Aug 1982 (300), 9 Jul 1984 (304); NEMP Sta. 17, 14 Aug 1981 (11); NEMP Sta. 18, 9 Dec 1979 (2 ABF, 56), 1 Jul 1980 (143), 2 Dec 1980 (7), 8 Jul 1981 (41), 5 Feb 1982 (35), 2 Sep 1982 (24), 6 Jul 1984 (34); NEMP Sta. 19, 15 Jul 1981 (1), 27 Jan 1982 (19); NEMP Sta. 22, 31 Jan 1982 (1), 5 Jul 1984 (2 ABF); NEMP Sta. 23, 17 Sep 1979 (6); NEMP Sta. 31, 10 Jul 1984 (1 ABF); NEMP Sta. 33, 13 Dec 1979 (550), 1 Aug 1980 (532), 5 Dec 1980 (177), 13 Aug 1981 (361 USNM 146120, 694 ABF), 6 Feb 1982 (6 ABF, 839), 1 Sep 1982 (822), 29 Aug 1984 (497), 16 Jul 1985 (149); NEMP Sta. 34, 9 Dec 1979 (62), 14 Jul 1980 (202), 2 Dec 1980 (70), 7 Jul 1981 (40), 27 Jan 1982 (107), 8 Sep 1982 (57), 7 Jul 1983 (91), 22 Jun 1985 (119); NEMP Sta. 35, 14 Jul 1980 (5), 21 Jul 1981 (7), 29 Jan 1982 (5), 16 Sep 1982 (2), 3 Jul 1984 (3), 25 Jun 1985 (14); NEMP Sta. 36, 2 Dec 1980 (110), 22 Jul 1981 (86), 26 Jan 1982 (95), 15 Sep 1982 (64), 1 Jul 1983 (177), 22 Jun 1985 (35); NEMP Sta. 37, 10 Jul 1980 (112), 11 Dec 1980 (37 ABF, 8), 16 Jul 1981 (67 ABF, 98), 27 Jan 1982 (27 USNM 146121, 76 ABF, 165), 28 Aug 1982 (1 ABF, 334), 6 Jul 1983 (583), 3 Jul 1984 (1 USNM 146122, 27 ZMUC, 125 ABF), 24 Jun 1985 (239); NEMP Sta. 39, 12 Jul 1980 (36); NEMP Sta. 15A, 23 Apr 1978 (4), 18 Jul 1979 (1), 11 Dec 1979 (1), 4 Dec 1980 (5), 2 Sep 1982 (12), 31 Aug 1984 (16), 14 Jun 1985 (21); NEMP Sta. 16B, 30 Jul 1980 (1), 12 Aug 1981 (2), 9 Sep 1982 (2); NEMP Sta. 16C, 12 Dec 1979 (25), 31 Jul 1980 (9 ABF, 73), 5 Feb 1982 (10); NYB Sta. 1, 28 Jul 1980 (11), 10 Aug 1981 (15), 12 Sep 1982 (123), 20 Jul 1983 (125), 24 Aug 1984 (88), 1 Oct 1985 (75); NYB Sta. 2, 28 Jul 1980 (6 ABF, 3), 10 Aug 1981 (3), 11 Sep 1982 (18), 20 Jul 1983 (6), 24 Aug 1983 (13), 15 Aug 1984 (15), 30 Sep 1985 (26); NYB Sta. 3, 28 Jul 1980 (3), 12 Sep 1982 (1); NYB Sta. 4, 2 Oct 1985 (1); NYB Sta. 5, 4 Aug 1980 (1), 9 Sep 1982 (1), 31 Aug 1984 (2), 1 Oct 1985 (4); NYB Sta. 8, 31 Jul 1980 (9), 15 Aug 1981 (7), 10 Sep 1982 (333), 20 Jul 1983 (38), 26 Aug 1983 (23), 2 Oct 1985 (1); NYB Sta. 9, 30 Jul 1980 (4), 12 Aug 1981 (1), 10 Sep 1982 (128), 25 Aug 1984 (199), 1 Oct 1985 (7); NYB Sta. 10, 30 Jul 1980 (321), 15 Aug 1981 (12), 13 Sep 1982 (52), 20 Jul 1983 (56), 25 Aug 1982 (62), 2 Oct 1985 (74); NYB Sta. 11, 30 Jul 1980 (21 ZMUO, 20 ABF), 12 Aug 1981 (8), 13 Sep 1982 (32), 25 Aug 1984 (18), 2 Oct 1985 (17); NYB Sta. 12, 30 Jul 1980 (142), 25 Aug 1984 (8); NYB Sta. 13, 31 Jul 1980 (625), 12 Aug 1981 (68), 13 Sep 1982 (1280), 21 Jul 1983 (437), 31 Aug 1984 (129), 2 Oct 1985 (153); NYB Sta. 14, 1 Aug 1980 (123), 13 Aug 1981 (20), 14 Sep 1982 (124), 5 Sep 1983 (112), 28 Aug 1984 (113), 3 Oct 1985 (175); NYB Sta. 16, 1 Aug 1980 (109), 12 Aug 1981 (11), 13 Sep 1982 (276), 20 Jul 1983 (14), 5 Sep 1983 (339), 30 Aug 1984 (27 ABF, 142), 2 Oct 1985 (85); NYB Sta. 17, 1 Aug 1980 (1 ABF, 10), 12 Aug 1981 (28), 13 Sep 1982 (140), 20 Jul 1983 (213), 5 Sep 1983 (118), 30 Aug 1984 (49), 2 Oct 1985 (42); NYB Sta. 18, 31 Jul 1980 (38), 10 Sep 1982 (93), 19 Jul 1983 (47), 25 Aug 1983 (14), 31 Aug 1984 (2), 1 Oct 1985 (65); NYB

Table 4.—*Lumbrineris hebes*: relationship of pygidium appendages to size.

Width in mm	0.09*	0.01–0.14	0.15–0.19**	0.20–0.24	0.25–0.29***	0.30–0.35	0.35–0.39	0.4–0.44	0.45–0.49	0.5–0.59	0.6–0.69	0.7–0.72
1–4 lobes	2	4	9	16	5	3	1	1	1	1	1	1
1 anal cirrus			2	4	3	2						
2 anal cirri		1	8	20	8	15	1	7	4	2	1	
3 anal cirri			1	1		1	1	1	1	1		
4 anal cirri				1	2	1	4	4		4	4	3

* Specimen: 0.9 mm by 0.09 mm; with 8 setigers; setiger 1 with 2 limbate setae; posterior postsetal lobe not elongated; pygidium with single lobe.

** Specimen: 1.9 mm by 0.2 mm; with 14 setigers; setiger 1 with 2 limbate setae and 1 slender-bladed, hooded hook; posterior postsetal lobe not elongated; pygidium with 4 lobes.

*** Specimen: 3.6 mm by 0.25 mm; with 48 setigers; setiger 1 with 2 limbate setae and 1 long, slender hooded hook; posterior postsetal lobe elongated; pygidium with 2 anal cirri.

Sta. 21, 13 Sep 1982 (4), 31 Aug 1984 (1), 30 Sep 1985 (3); NYB Sta. 22, 9 Sep 1982 (64), 5 Jul 1983 (12), 31 Aug 1984 (10), 1 Oct 1985 (7); NYB Sta. 24, 3 Aug 1980 (31), 14 Aug 1981 (28), 14 Sep 1982 (16); NYB Sta. 28, 13 Aug 1981 (11), 14 Sep 1982 (18), 28 Aug 1984 (2 ABF); NYB Sta. 31, 1 Oct 1985 (6); NYB Sta. 32, 1 Oct 1985 (1); NYB Sta. 33, 15 Sep 1982 (2), 30 Aug 1984 (1), 30 Sep 1985 (10); NYB Sta. 34, 29 Jul 1980 (1), 9 Sep 1982 (14), 7 Sep 1983 (23), 30 Aug 1984 (19), 1 Oct 1985 (25); NYB Sta. 35, 29 Jul 1980 (5 ABF), 9 Sep 1982 (2), 21 Jul 1983 (2), 30 Aug 1984 (2), 1 Oct 1985 (3); NYB Sta. 37, 9 Sep 1982 (2); NYB Sta. 39, 1 Aug 1980 (29), 11 Aug 1981 (37), 9 Sep 1982 (44), 6 Sep 1983 (29), 30 Aug 1984 (11), 3 Oct 1985 (20); NYB Sta. 40, 31 Jul 1980 (304), 12 Aug 1981 (2 ABF, 68), 9 Sep 1982 (696), 19 Jul 1983 (9), 1 Oct 1985 (33); NYB Sta. 42, 4 Aug 1980 (20), 15 Aug 1981 (101), 2 Oct 1985 (3); NYB Sta. 43, 31 Jul 1980 (179), 15 Aug 1981 (381), 13 Sep 1982 (69), 13 Jul 1983 (34); NYB Sta. 44, 31 Jul 1980 (55), 14 Sep 1982 (61), 21 Jul 1983 (18), 2 Oct 1985 (1); NYB Sta. 64, 31 Aug 1984 (1); NYB Sta. 65, 11 Sep 1982 (326).—Off Delaware, Philadelphia Dumpsite: EPA Sta. 201, 38°20′N, 74°18′W, 51 m, Jun 1983 (12), coll. Cove Corporation, Lusby, Maryland, N. K. Mountford ID.

Description.—Preserved material colorless. In life color pale yellow, intestines yellow, orange or blood red (Moore, 1900:472). NYB specimen (USNM 146122) 15 mm long, 0.6 mm wide, with 121 setigers. Body width increases slightly in first 10–15 setigers then tapers gradually towards posterior end. Prostomium about as long as wide, either acorn-shaped (Fig. 9a) or conical. Peristomial rings equal to each other and to first setiger. Postsetal lobes bluntly conical and slightly longer than presetal lobes in anterior (Fig. 9b) and median setigers (Fig. 9c), much longer, digitate in posterior setigers and directed obliquely upwards (Fig. 9d). Presetal lobes rounded throughout. About 30–40% of mature specimens with an indistinct notopodial rudiment on first 25–30 setigers. Pygidium varying greatly from juveniles to adults, having from 4 lobes (Fig. 10a) to 1–4 anal cirri (Fig. 10b–e), with 4 or 2 anal cirri most common (Table 4).

Anterior parapodia of mature specimens with 4 (rarely 5) limbate setae in superior position, then 1–2 long slender simple hooded hooks followed by a single limbate seta. Limbate setae less numerous after setiger 10, totally lacking after setigers 17–24. Setigers 10–11 with transitional shorter hooks with slender blades; setigers 12 through posterior with 2–3 short hooks with bulbous tips. Hooks of anterior setigers (Fig. 8e) with 8–9 teeth of equal size, main fang slightly larger than adjacent tooth. Hooks become bulbous with 8–9 teeth in median setigers (Fig. 9f), and 6–7 teeth in posterior ones (Fig. 9g); teeth decreasing apically in

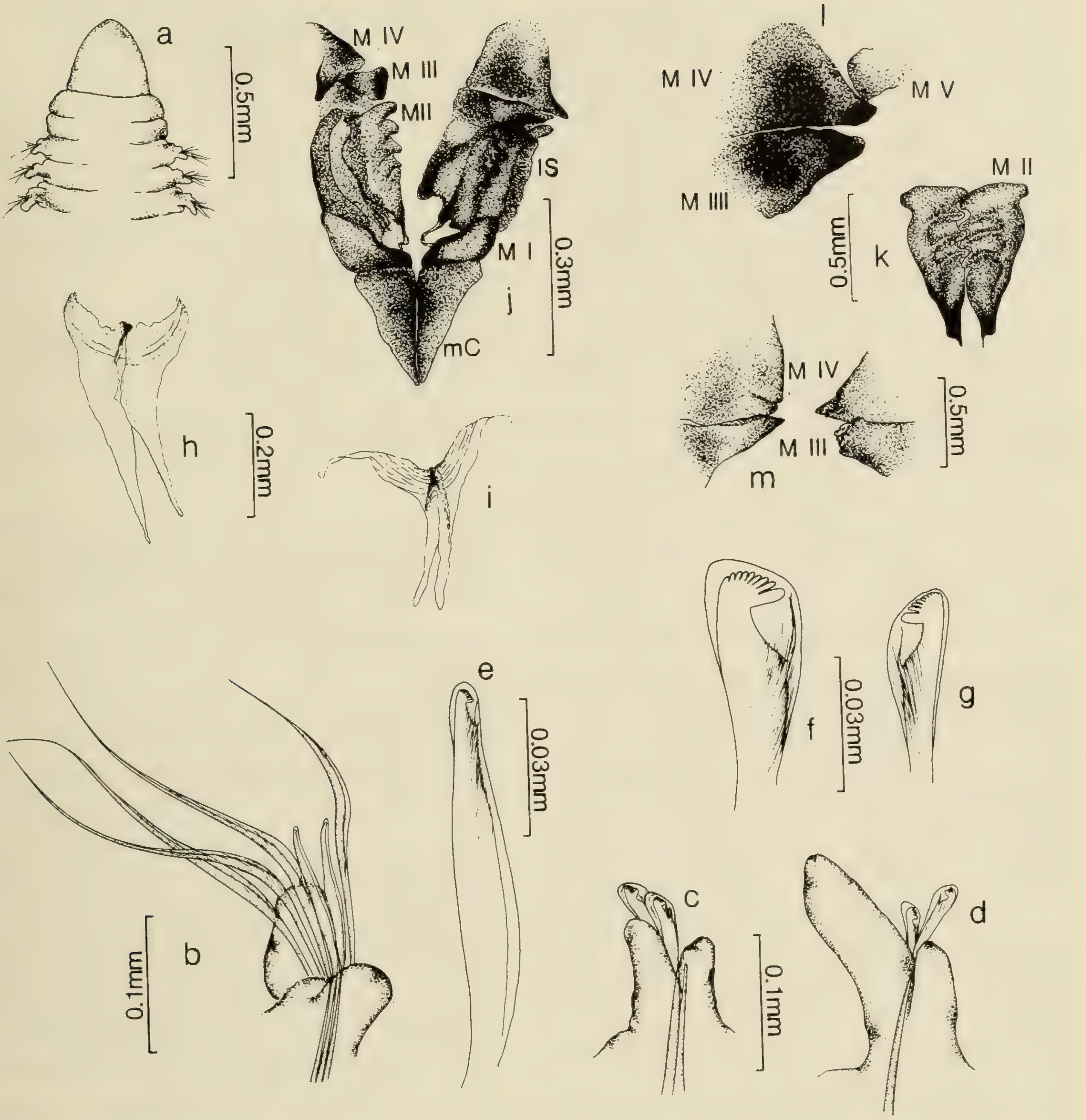

Fig. 9. *Scoletoma hebes*: a, Prostomium; b, Right parapodium 3; c, Parapodium 27; d, Posterior parapodium; e, Hooded hook from parapodium 4; f, Hook from parapodium 27; g, Hook from posterior parapodium; h, Mandibles; i, Mandibles combined with fleshy material; j, Maxillae; k, M II; l, Right M III, M IV and M V; m, M III and M IV, showing tooth dentition and erosion (from same specimen).

size, main fang usually entire. Aciculae yellow, 3 (rarely 4) in anterior setigers, 1 in posterior setigers.

Mandibles (Fig. 9h) paper thin, fragile and translucent invisible in some individuals. Anterior flared wings of many mature individuals cannot be entirely separated from fleshy parts (Fig. 9i). Mandible blades divided for one third to two thirds of their length. Maxillary apparatus brown and fragile, especially M III and M IV. Maxillary carriers broad, slightly constricted near distal end, permanently divided (Fig. 9j); M I forceps stout with smooth border below falcate tip with strong lateral supports; M II asymmetrical with 4 (3–5) teeth, distal tooth largest, tooth below almost as large (Fig. 9k); M III and M IV with long blunt tooth (Fig. 9l). Occasionally in specimens found in coarse sands, tooth of M III and/or M IV

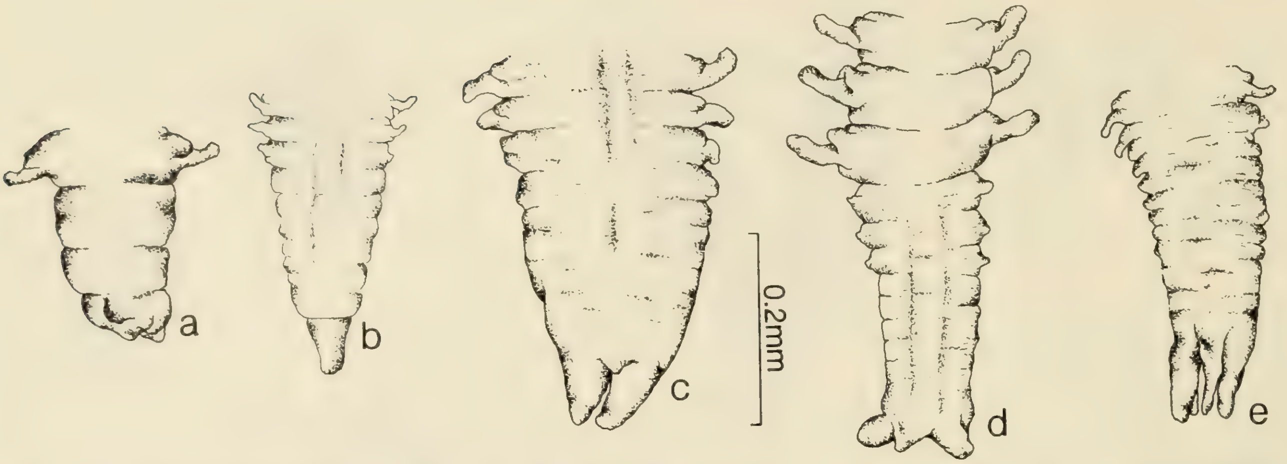

Fig. 10. Growth variations of pygidium in *Scoletoma hebes*: a, 4 lobes; b, Single lobe; c, 2 anal cirri; d, 3 anal cirri; e, 4 anal cirri.

worn down or broken, giving appearance of more than one tooth (Fig. 9m). M V lightly joined to M IV just above blunt tooth.

Remarks.—Identification of this species is difficult due to the confusion existing in the literature. Verrill's original description lacked illustrations, and did not mention the mouthparts or the number of anal cirri. Moore (1900) described *S. hebes* as having 1 larger tooth and 2–3 smaller teeth on M III and 1 or 2 teeth on M IV. His illustrations of the maxillary apparatus show the same fragmentation of M III and IV as we have observed in specimens from coarse sands.

Pettibone (1963:264) used Moore's illustration of *S. hebes* as part of her figures of *S. tenuis,* with the description of *S. tenuis* reading: "Simple hooded hooks beginning on or about setiger 9 (1–17)."

Perkins (1979:436–439) reexamined the syntypes and published a fairly complete redescription of *S. hebes*; however, due to the limited number (7) of specimens available for examination, the pygidium was described as having four rounded lobes. As also pointed out by Perkins, *S. hebes* may be distinguished from *S. tenuis* by the long slender hooded hooks which start on setiger 1; *S. tenuis* has short bulbous hooks, which start on setigers 10–13 in adults and on setigers 8–9 in juveniles.

Separation of the northern *S. hebes* and the southern *S. verrilli* (Perkins, 1979) is more difficult and requires examination of M III and M IV. In *S. verrilli,* the distal silhouette of M IV is conical or gum drop-shaped (Perkins 1979, fig. 11f) rather than riding hat-shaped; the inferior midway point of M IV touches at M III. Perkins described M IV as having a large semi-oval M V (not drawn), but the M V was not present in 12 specimens from Biscayne Bay, Florida (Florida Department of Environmental Regulation, Sta. 36, 25°46′N, 80°11′W, 2.5 m, Oct 81 (24), H. D. Rudolph ID, ABF coll.) or in 1 specimen from Texas, off Port Isabel, BLM Sta. IV–I, 20°10′N, 97°01′W, 27 m, fall 1977 (53), J. M. Uebelacker ID, USNM 90992. The specimens from Biscayne Bay were thinner in proportion to length compared to *S. hebes,* and had 0, 1 or 2 anal cirri.

Scoletoma hebes is sometimes confused with *S. impatiens* (Claparède, 1868), which has a similar long slender hook starting on setiger 1, but *S. impatiens* has 2 teeth on M III and a short posterior postsetal lobe.

Distribution.—Gulf of Maine to Gulf of Mexico; 8–110 m. Grain size range from granular to very fine silt; greatest numbers at NYB Stations in very fine sand. TOC values from 0.3–34.4 mg/g; most abundant at stations where TOC values are greater than 7.0.

Scoletoma tenuis (Verrill, 1873), new combination

Lumbriconeris tenuis Verrill, 1873:594–595; 1879:49.

Lumbrinereis tenuis.—Webster & Benedict, 1884:594–595; 1879:49.

Lumbrineris tenuis.—Hartman, 1944b:340, pl. 49, figs. 3–5.—Pettibone, 1963:264 (in part), fig. 70a–d.—Gardiner, 1976:199, fig. 26p–r.—Perkins, 1979:433–436, fig. 7a–j.—Uebelacker, 1984:26–28, figs. 21, 22a–g.

Lumbrineris bassi.—Hartman, 1944a:150–151, pl. 10, figs. 217–222.

Material examined.—Northwestern Atlantic, Off NE USA: NEMP Sta. 2, 6 Dec 1980 (1 ABF); NEMP Sta. 3, 11 Jul 1981 (1 ABF).—Connecticut, Off Noank: Long Island Sound Survey, Sta. 139, 41°00.02′N, 72°00′W, 21 m, 14 Aug 1972 (4 ABF).—New Jersey, Manasquan River: New Jersey Department Fish, Game and Wildlife, Manasquan River Survey, 1 m, Oct 1986 (9 ABF), C. Idelberger ID.

Remarks.—Moore (1900:463–465) was the first to provide a complete description and drawings of *S. tenuis.* Excellent recent descriptions are given in Perkins (1979:433–436) and Uebelacker (1984:Ch. 41, pp. 26–28). Differences between *S. tenuis* and *S. hebes* are given under the remarks of *S. hebes.*

Distribution.—Massachusetts to Gulf of Mexico; intertidally–24 m. Grain sizes in our survey range from fine sand to very fine sand. TOC values 1.3–5.9 mg/g.

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A NEW SPECIES OF *DENTATISYLLIS* (SYLLIDAE: POLYCHAETA) FROM CAPE VERDE ISLANDS, WEST AFRICA

Eduardo López García and Guillermo San Martín Peral

Abstract.—*Dentatisyllis junoyi,* a new species of Syllinae (Syllidae: Polychaeta) from the Cape Verde Islands off the Atlantic coast of Africa, is described. This species is characterized by having blades of short spiniger-like setae with rounded and indistinctly bifid tips and blades of falcigers with the proximal tooth larger than the distal tooth and the margin with long, distally directed subdistal spines.

The only work exclusively devoted to polychaete annelids from the Cape Verde Islands to date is that of Rullier (1964). Other works that mention species from these islands are those of McIntosh (1885), Fauvel & Rullier (1957, 1959b) and Kirkegaard (1983). A third group dealing more generally on species from the western coast of Africa are those of Augener (1918), Fauvel (1953), Fauvel & Rullier (1959a), Day (1967), and Hartmann-Schröder (1974).

Samples containing the new species of *Dentatisyllis* reported herein were collected during the "I Expedición Ibérica" to the archipelago in August, 1985. A provisional list of polychaetes found in these samples now includes about 70 species. The generic diagnosis for *Dentatisyllis* was given by Perkins (1981), and is not included here.

Specimens of the type series have been preserved in permanent microscopic slides in glycerine jelly except for the holotype and are deposited in the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Madrid, Spain. The holotype is preserved in 70% ethanol.

Descriptions, measurements, and figures have been prepared with the use of a compound microscope provided with differential interference-contrast optics (Nomarsky) and a camera-lucida drawing tube. Measurements reported are from the holotype; length measurements do not include antennae and anal cirri; width measurements were taken across the proventricular level and do not include parapodia, setae, and dorsal cirri.

Family Syllidae Grube, 1850
Subfamily Syllinae Grube, 1850
Genus *Dentatisyllis* Perkins, 1981
Dentatisyllis junoyi, new species
Fig. 1A–M

Material examined.—Cape Verde Islands: Off Curral Velho (15°58′N, 22°48′W; Boavista Island); sand; 15 m depth; holotype (MNCNM, 1601/802). Off Salamanza (16°54′N, 24°57′W; Sao Vicente Island); *Halimeda*; 3 paratypes (MNCNM, 1601/803).

Etymology.—The species is named in honor of Dr. Juan Junoy Pintos, Departamento de Biología Animal, Universidad de Alcalá de Henares, eminent benthologist who has also worked on polychaetes.

Description.—Body long, slender, cylindrical, without color markings, 5.2 mm long, 0.24 mm wide, 55 setigers. Prostomium oval, wider than long, with 4 eyes in open trapezoidal arrangement. Eyespot not seen. Palps stout and triangular, fused dorsally at bases, somewhat longer than prostomium. Median antenna originating on about middle of posterior half of prostomium, nearly twice as long as lateral antennae and longer than prostomium and palps together, with 17 articles (up to 22 in paratypes), on short ceratophore; lateral antennae with 11–12 articles (up to 15 in paratypes), originating near anterior margin of prostomium. Peristomial segment laterally distinctly separated from prostomium, dorsally covered by first setiger; dorsal tentacular cirri 1.5–2 times longer than ventral tentacular cirri, with 13–17 articles; ventral tentacular cirri with 7 articles (Fig. 1A). Dorsal cirri of first setiger longer than median antenna, with about 20 articles. Dorsal cirri of midbody segments all longer than body width, alternating in length; short cirri with 7–9 articles; long cirri with 14–17 articles (Fig. 1C). Articles of dorsal, tentacular, and anal cirri and antennae with greenish, spiral-shaped inclusions. Parapodia short and cylindrical. Ventral cirri digitiform, longer than parapodial lobes (Fig. 1C). Anterior parapodia each with about 8–12 compound heterogomph setae, blades slender, bidentate, with distal teeth somewhat hooked and margin provided with short spines; 2–3 uppermost spines very long extending to proximal tooth; blades of setae of anterior segments markedly differing dorsally to ventrally in length and shape; 24 μm above, diminishing to 13 μm below; proximal tooth of blades of setae longer than distal tooth, even longer ventrally (Fig. 1D). Toward midbody uppermost 1–2 blades of compound setae progressively more slender and proportionally longer, becoming spiniger-like, distally becoming rounded and indistinctly bidentate, with spines on margin short except distally (Fig. 1F). Blades of falcigers of midbody segments numbering 4–6 per parapodium, with short distal tooth and long, hooked proximal tooth, with slight dorso-ventral gradation in length, 17 μm above, 13 μm below (Fig. 1G). Anterior parapodia each with 2–3 acicula (Fig. 1E); acicula of posterior parapodia single, acuminate (Fig. 1K). Dorsal simple seta on posterior parapodia solitary, thin, with 2 similar teeth and short subdistal spines (Fig. 1L); ventral simple seta on far posterior setigers, solitary, stout, bidentate with small distal tooth and large proximal tooth (Fig. 1M). Pharynx long, extending through about 6½ segments in holotype (up to 8½ segments in paratypes) anterior middorsal tooth on anterior margin; anterior end of pharynx surrounded by 10 large, soft papillae and provided with a crown of 20 small teeth, only sharply seen in a paratype (Fig. 1N). Proventriculus similar in length to pharynx, extending through about 4 segments, with about 27 rows of muscle cells (Fig. 1A). Pigidium small, with 2 long moniliform anal cirri each with about 11 articles, and a short ventral appendage (Fig. 1B).

Remarks.—*Dentatisyllis junoyi* is characterized by having falcigers with an enlarged proximal tooth long subdistal spines on the distal margin of the blade, by having spiniger-like setae on middle and posterior setigers also with long subdistal spines and with bidentate tips, teeth of spiniger-like setae progressively decreasing in size and appearing rounded on median-posterior and posterior parapodia. Several species of the genus *Syllis* Lamarck, 1818 have similar falcigers but lack spiniger-like setae: *Syllis regulata* (Imajima 1966:285) differs further by having apparently unidentate dorsal simple setae and much longer cirri; *Syllis glarearia* (Westheide 1974:55) has much longer dorsal cirri and has dorsal simple setae that apparently lacks serrations; *Syllis* sp. A (Uebelacker 1984:30–134) has compound setae with enlarged blades in midbody setigers and strongly serrated ventral simple setae. Besides having falcigerous setae similar to those of *D. junoyi, Syllis lutea* (Hartmann-Schröder 1960:81, Campoy 1982: 428, San Martín 1984:370) has long-bladed falcigers with well developed serrations on blade margin, but blades have well marked distal and subdistal teeth and ventral simple setae have no enlarged proximal tooth. *Syllis cruzi* (Núñez & San Martín 1991:236) is the most similar to the new species differing only in lacking spiniger-like setae and de-

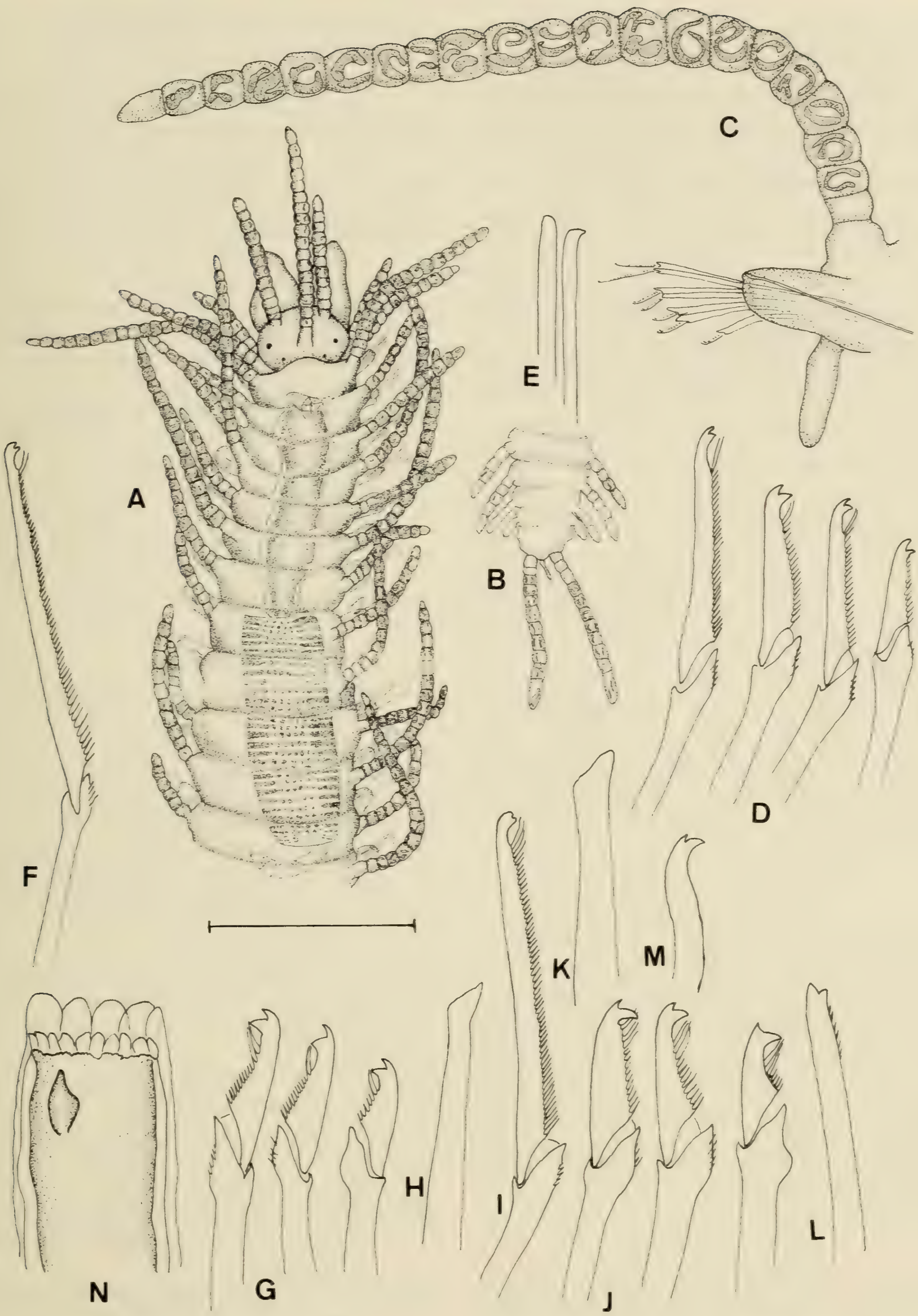

Fig. 1. *Dentatisyllis junoyi,* n. sp.: A, Anterior end, dorsal view; B, Posterior end, dorsal view; C, Midbody parapodium; D, Falcigerous setae of anterior parapodium; E, Acicula (same parapodium as D); F, Spiniger-like setae of median parapodium; G, Falcigerous setae (same parapodium as F); H, Aciculum (same parapodium as F); I, Spiniger-like seta of posterior parapodium; J, Falcigerous setae (same parapodium as J); K, Aciculum (same parapodium as J); L, Dorsal simple seta (same parapodium as J); M, Ventral simple seta of far posterior parapodium; N, Anterior end of pharynx. Scale: A, B: 1.97 mm; C: 0.64 mm; D, E, F, G, H, I, J, K, L, M: 20 μm; N: 0.64 mm.

tails of falcigerous blades. Anterior rim of pharynx of all these species has not been examined to study the presence of denticles; perhaps some of them could belong to the genus *Dentatisyllis.* The following species of *Syllis* have spiniger-like setae that are similar to *D. junoyi*: *Syllis* cf. *lutea* of Uebelacker (1984:30–136) has spiniger-like setae with short teeth, ventral simple setae that have short proximal teeth and falcigers that do not have long spines on the margin of the blade; and *Syllis rosea* (Langerhans 1879: 538, Imajima 1966:529, Campoy 1982:395, San Martín 1984:335) has spiniger-like setae with rounded tips on posterior setigers but has dorsal simple setae that are truncated, ventral simple setae that have a short proximal tooth, acicula that are bluntly rounded and falcigers that have a short proximal tooth. *Dentatisyllis carolinae* (Day 1973:30, Perkins 1981:1166, Uebelacker 1984:30–115) has falcigerous setae very similar to those of *D. junoyi* but lacks spiniger-like setae and has much longer cirri, truncate dorsal simple setae, serrate ventral simple setae and 10 teeth on the pharyngeal margin instead of 20.

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A NEW ARABELLID POLYCHAETE LIVING IN THE MANTLE CAVITY OF DEEP-SEA WOOD BORING BIVALVES (FAMILY PHOLADIDAE)

Harlan K. Dean

Abstract.—A new species of polychaete, *Pholadiphila turnerae* (Family Arabellidae), is described from the mantle cavity of two species of wood boring bivalves (Family Pholadidae, Subfamily Xylophagainae). This is the first reported association between an arabellid polychaete and a mollusk. This species shows reductions in jaw structure and setal development similar to the reductions observed in many endoparasitic arabellids. The jaw apparatus consists of three pair of maxillae, a short, slender maxillary carrier, and well-developed mandibles. Setae are of three types: acuminate, capillary and spinous. Ecological aspects of commensal/parasitic polychaetes living in a bivalve mantle cavity are discussed.

Woody plant material washed into the deep sea is rapidly decomposed by wood boring bivalves of the family Pholadidae, subfamily Xylophagainae, and acts as a center for organic enrichment communities at abyssal depths (Turner 1973, 1977, 1981; Wolff 1976; Grassle 1987). As part of a long-term study of these communities by Dr. Ruth Turner, the DSRV *Alvin* has been utilized to place "wood islands" and associated wood panels in the deep sea and recover them after varying periods of time. While studying the polychaetes associated with the recovered wood panels, several specimens were encountered living in close association with the wood boring bivalve mollusks. Specimens of two members of the subfamily Xylophagainae (Family Pholadidae), *Xyloredo ingolfia* Turner, 1972 and an as yet undescribed genus and species (Turner, pers. comm.) were found to harbor a previously undescribed species of Arabellidae within their infrabranchial chamber (Fig. 3A). This paper describes the arabellid species, *Pholadiphila turnerae,* and discusses its ecology.

Family Arabellidae Hartman, 1944
Pholadiphila, new genus

Diagnosis.—Body slender, elongate, flattened dorso-ventrally, segmentation distinct. Prostomium small, conical, antennae and palps absent, eyespots lacking. Prostomium indistinctly separate from the first segment. Peristomial ring indistinct. Three pairs of equal maxillae; MI falcate, bifid; MII ctenoid with appressed, blade-like processes; MIII small avicular. Maxillary carrier short, slender tripartite anteriorly. Mandibular plates large, smooth, shield-like; united medially. Parapodia uniramous, conical, cirri absent. Setae simple, 3 types: stout, emergent spines (Fig. 3C); more slender acuminate setae (Fig. 3D); and capillary setae (Fig. 3B).

Remarks.—The Arabellidae Hartman, 1944 and Oenonidae Kinberg, 1865 (emended by Colbath 1989a) are separated from other eunicoids by their prionognath jaw pattern and the possession of unmineralized jaws (Colbath 1989a). The prionognath jaw pattern is characterized by two long, slender maxillary carriers and what is usually termed a ventral "third carrier" (or ligament by Colbath [1986]). Three genera of predominantly endoparasitic arabellids are exceptional in that the maxillary carriers are fused along much of their length while the third carrier may (*Haematocleptes* Wirén, 1886, *Labrorostratus* Saint-Joseph, 1888) or may not (*Oligognathus* Spengel, 1882) be evident. The possession of a slender maxillary carrier with indications of a tripartite anterior end (Fig. 2E) by *Pholadiphila turnerae* strongly suggests fusion of what was originally a prionognath maxillary carrier pattern. The reduced number of maxillae and the fused, short (but not broad) maxillary carrier are believed to be the consequence of a commensal or parasitic lifestyle similar to the jaw reductions seen in other parasitic genera within the Arabellidae. The small jaw apparatus of *P. turnerae* is a translucent amber structure showing no indication of the mineralization seen in labidognath jaws, again in agreement with the prionognath jaw type.

In addition to jaw structure, several other characteristics associate *P. turnerae* with the family Arabellidae. Arabellids are characterized as having a cylindrical body of nearly uniform width, a reduced prostomium lacking appendages and uniramous parapodia (Hartman 1944). Members of the Oenonidae Kinberg, 1865 (emended by Colbath 1989a), which also have prionognath jaws, differ from *P. turnerae* in the possession of one to three antennae, elongate postsetal lobes, prominent dorsal cirri, and geniculate setae (Colbath 1989a).

Hartman (1944) described the Arabellidae as possessing simple, limbate setae sometimes accompanied by projecting acicular spines (or ventral setae [Colbath 1989b]). Capillary setae have also been described for some of the parasitic species of Arabellidae (Pettibone 1957). The thick emergent spines and capillary setae of *P. turnerae* are both compatible with its inclusion within the Arabellidae. The characteristic limbate setae are absent in this species, probably due to setal modifications correlated with its lifestyle. Similar reductions in setae have generally been associated with commensalism in the Polychaeta (Blake 1990) and with parasitism in other members of the Arabellidae (Pettibone 1963, Uebelacker 1984).

Pholadiphila turnerae, new species
Figs. 1–3

Material examined.—WHOI Deep Ocean Station No. 2: 38°17.5′N, 69°35.2′W, 3602 m. Wood Panel N-30; submerged 5 Sep 1975 (*Alvin* Dive 601), recovered 23 Sep 1977 (*Alvin* Dive 790): HOLOTYPE (USNM 145086) removed from the infrabranchial cavity of *Xyloredo ingolfia* Turner 1972 (Family Pholadidae). Paratype (USNM 145087) specimen with anterior end extending out of the exhalent siphon of a pholad belonging to an undescribed genus of the subfamily Xylophagainae. Paratype (MCZ 20008) specimen with anterior end extending out of the excurrent siphon of a pholad belonging to an as yet undescribed genus of the subfamily Xylophagainae. Wash material from recovery box carrying panels N-30 and N-42; panels submerged 5 and 6 Sep 1975 (*Alvin* Dives 601 and 602, respectively), recovered 23 Sep 1977 (*Alvin* Dive 790): Paratype (USNM 145089). Wood Panel N-83; submerged 23 Sep 1977 (*Alvin* Dive 790), recovered 3 Aug 1980 (*Alvin* Dive 1031): Paratype (USNM 145088). WHOI Deep Ocean Station No. 1, 39° 45.3′N, 70°41.2′W, 1767 m. Wood Panel N-68; submerged 17 Aug 1976 (*Alvin* Dive 685), recovered 29 Jul 1977 (*Alvin* Dive 773): Paratype (MCZ 20009).

Description.—Specimens, preserved in alcohol, light yellow to buff. Body long and slender (Fig. 1A), flattened ventrally and weakly arched dorsally. Body tapered anteriorly from about setiger 10, sides parallel for most of body, tapered near the posterior end. Holotype 163 setigers, 15.4 mm long with maximum width 0.23 mm excluding

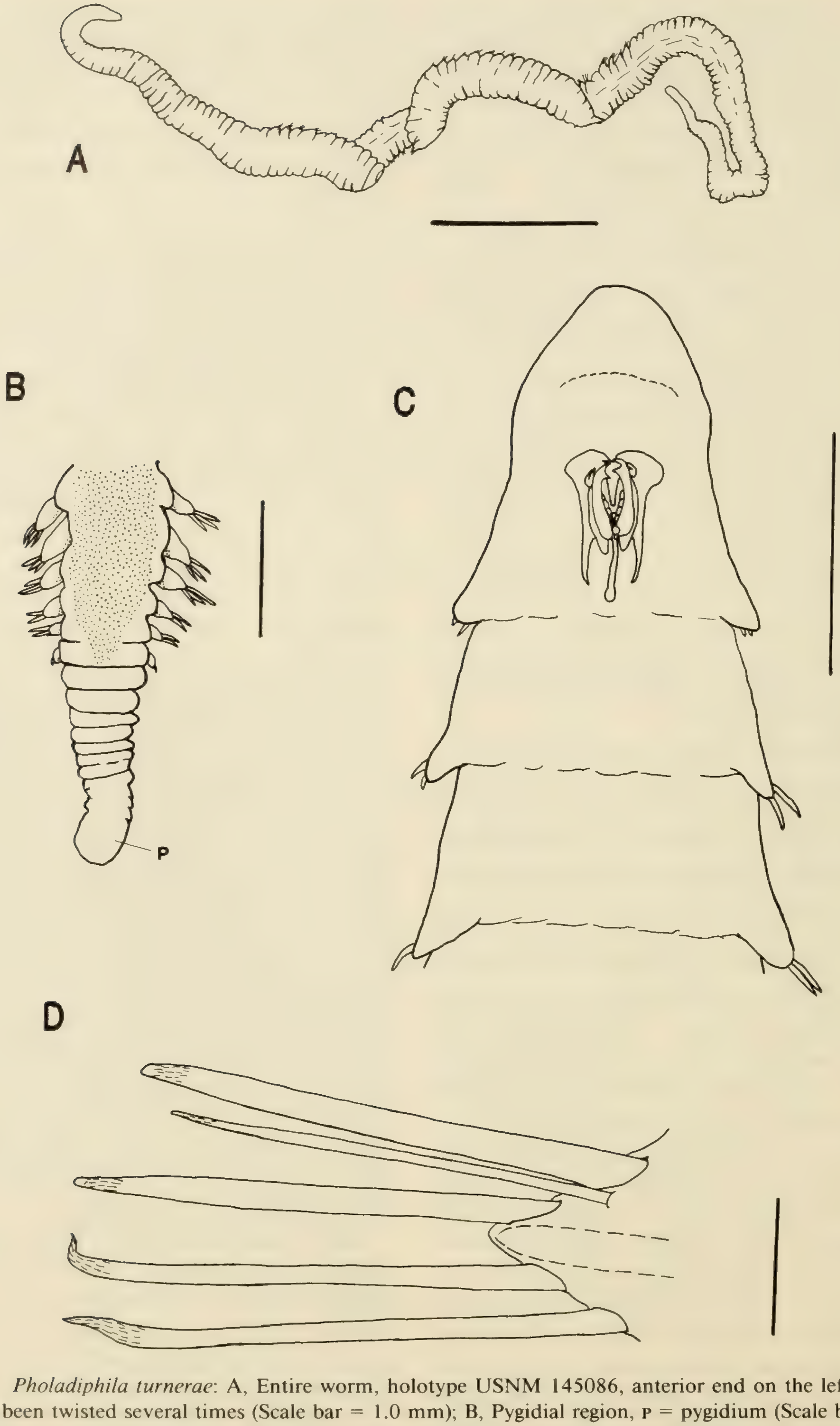

Fig. 1. *Pholadiphila turnerae*: A, Entire worm, holotype USNM 145086, anterior end on the left and the body has been twisted several times (Scale bar = 1.0 mm); B, Pygidial region, P = pygidium (Scale bar = 200 μm); C, Anterior end (Scale bar = 100 μm); D, Median parapodia, anterior view (Scale bar = 20 μm).

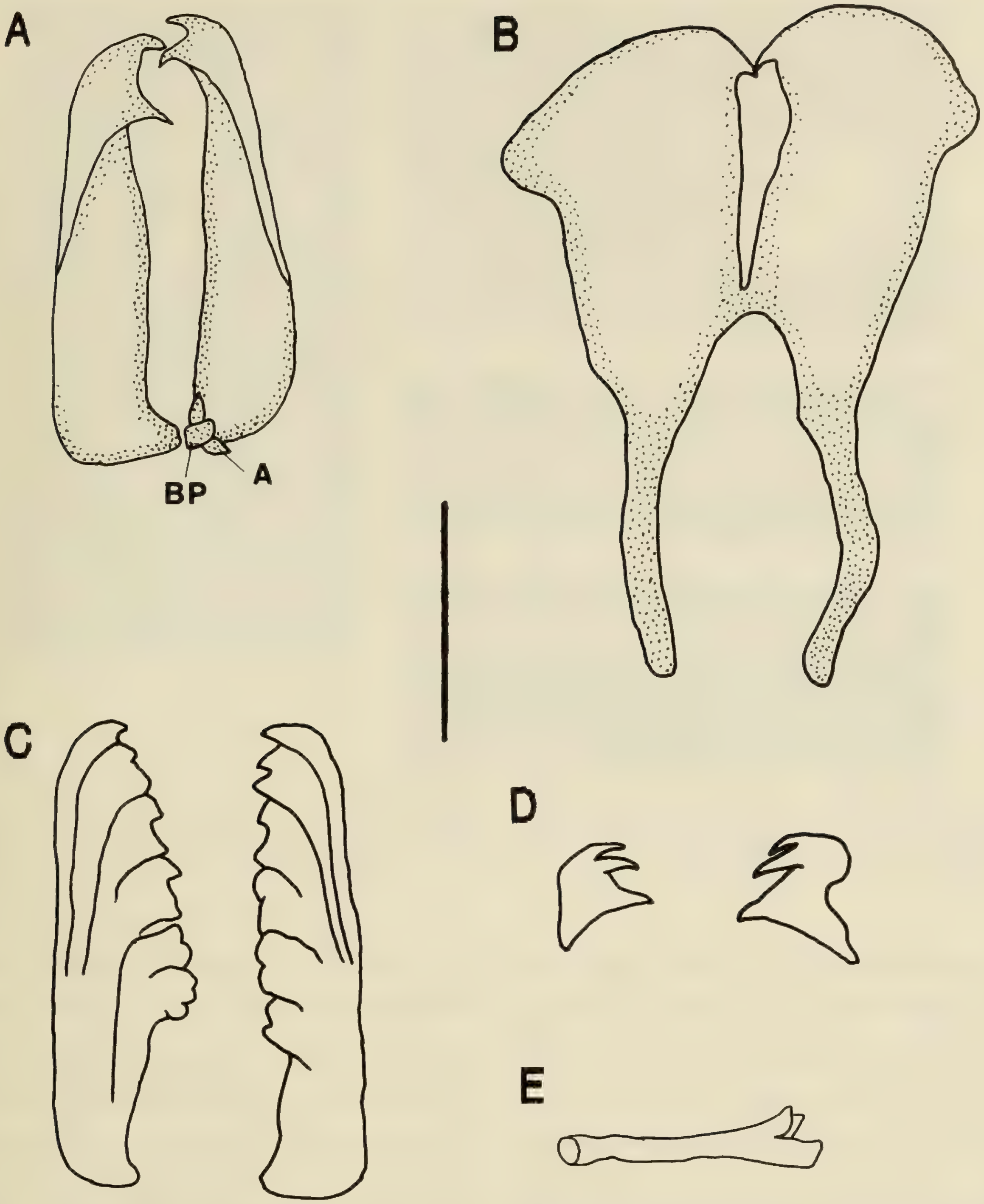

Fig. 2. Jaw apparatus of *Pholadiphila turnerae* drawn from a squash preparation of paratype MCZ 20009: A, Maxillae I, BP = basal plate, A = alae; B, Mandibles; C, Maxillae II; D, Maxillae III; E, Maxillary carrier (Scale bar = 20 μm).

parapodia. Largest specimen examined 262 setigers, 19.2 mm long with maximum width 0.27 mm excluding parapodia. Prostomium conical, indistinctly separated from setiger 1, antennae, palps, and eyespots absent (Fig. 1C). Prostomium and peristomium fused.

Cuticular jaw apparatus: 3 pairs of maxillae; MI gracile falcate, bifid with a pronounced gap between the falx and the smooth base (Fig. 2A), MIR with a thickened low cylindrical boss (basal plate, sensu Wolf 1980) possessing a pair of short alae; MII with 6 appressed, blade-like processes, 5 posterior with a pair of low bosses on the

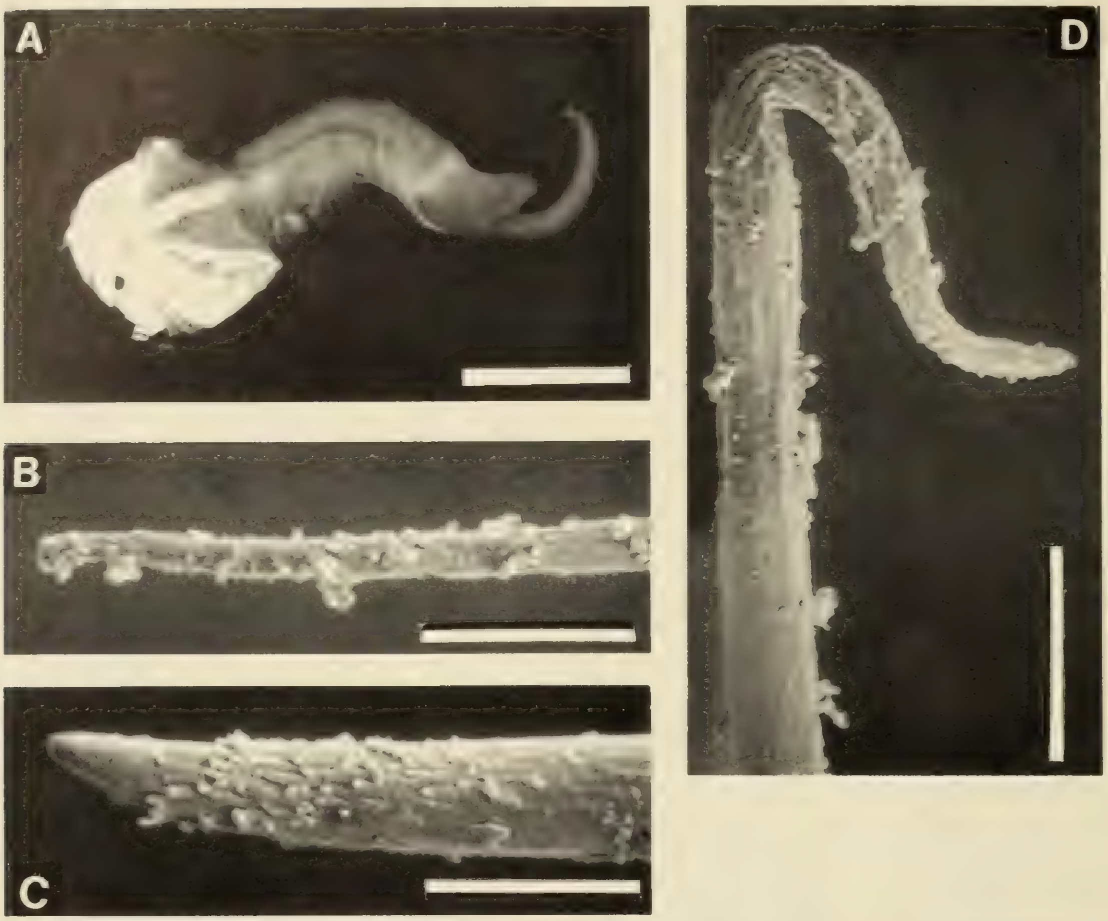

Fig. 3. *Pholadiphila turnerae*: A, paratype USNM 145087 with its anterior end extending from the siphonal opening of a specimen of an undescribed Xylophagainae (Family Pholadidae), most of the body may be seen coiled within the branchial chamber of the pholad (Scale bar = 1.0 mm); B, Capillary seta; C, Stout, emergent spine; D, Acuminate seta (Scale bars B–D = 5 μm).

medial border, basal portion unarmed, extending posterior to the base of MI (Fig. 2C); MIII small, avicular, with wide base and 2 sharply pointed teeth (Fig. 2D). Maxillary carrier slender, short (shorter than MI sensu Colbath 1989b), cylindrical, recurved, anterior with a pair of dorsal bosses and a single ventral extension (Fig. 2E). Mandibles a pair of large flat plates united posterio-medially; anterior border of each plate slightly convex with single weak tooth at anterio-medial margin (Fig. 2B); each mandible with a slightly curved, free end approximately equal in length to the plate.

Parapodia conical, with single stout acicula (Fig. 1D); with 1 stout spine (Fig. 3C) and a small, supra-acicular capillary seta (often broken) on setiger 1; 2 stout, supra-acicular spines on setiger 2; 2 supra-acicular stout spines and capillary seta (Fig. 3B) beginning on setiger 3; a stout, sub-acicular spine added at setiger 10; 2 stout, supra-acicular spines, a supra-acicular capillary seta and 2 sub-acicular acuminate setae (Fig. 3D) beginning at setiger 19 or 20 (the superior acuminate seta formed by transformation of one of the stout spines with intermediates occurring on setigers 18 and 19) and continuing to the pygidial region. Final setiger with two short, supra-acicular spines; 2 preceding setigers with 2 stout, supra-acicular spines and a sub-acicular, acuminate seta. Capillary and acuminate setae hirsute throughout, stout spines weakly hirsute posterior to setiger 20 (Fig. 3B–D). Posterior region with 7 (9 in the largest specimen examined) distinct, asetigerous segments and an undifferentiated cylindrical region anterior to the pygidium; anus terminal (Fig. 1B).

Etymology.—This species is named in honor of Dr. Ruth Turner in recognition of both her extensive work with the wood boring bivalve mollusks and the support and encouragement she has shown me.

Remarks.—In some respects *Pholadiphila turnerae* has a less reduced jaw apparatus than many of the parasitic genera in the Arabellididae. The well-developed, diamond-shaped mandibular plates that are fused along part of their length are similar to the mandibles of free-living arabellids. In the genera *Labrorostratus, Haematocleptes* and *Oligognathus* the mandibles are reduced to small plates and they are entirely absent in the parasitic species of *Drilonereis* Claparède, 1870. The 3 pairs of well-developed maxillae (MI falcate, MII and MIII toothed) of *P. turnerae* are most similar to those of the parasitic species of the genus *Drilonereis* that possess 4 pairs of maxillae and to those of the free-living arabellids which possess 5 pairs of well-developed maxillae. In the remaining parasitic genera, the maxillae of *Oligognathus* have been reduced to 3 pair of unidentate hooks while those of *Labrorostratus* and *Haematocleptes* have been reduced to 2 pair of small cuticular pieces.

Whereas the maxillae of *P. turnerae* are less reduced than those of several parasitic arabellids, its maxillary carriers are greatly modified. Free-living arabellids and both free-living and parasitic members of the genus *Drilonereis* possess a pair of long, slender maxillary carriers with a third carrier attached ventrally. The paired maxillary carriers have been fused in *Labrorostratus, Haematocleptes* and *Oligognathus* with the third carrier retained in the former two genera and lost in *Oligognathus.* The maxillary carriers of *Pholadiphila turnerae* are fused along their entire length and the ventral extension may represent a vestigial third carrier. There is also a size reduction in the maxillary carrier of *P. turnerae* being approximately equal in length to the maxillae while those of all other arabellids are much longer than the maxillae.

Reductions in the arabellid setal pattern are seen in the parasitic species *Drilonereis benedicti* Pettibone, 1957 which has no emergent setae and in the two species of the genus *Haematocleptes, H. terebellidis* Wirén, 1886 and *H. leaenae* Hartman & Fauchald, 1971, which possess slender, distally pointed setae rather than limbate setae. The setal arrangement of *Pholadiphila turnerae* agrees with that of the above mentioned species as all other members of the arabellids (parasitic or free-living) possess limbate setae with a well-developed blade (sensu Colbath 1989a). The acuminate setae and the strong spines of *P. turnerae* may be an adaptation to the parasitic or commensal existence of this species, affording strong purchase against the body of its molluscan host. These setae are more highly developed than the setae seen in other parasitic arabellids being more robust, more numerous and extending out much further from the parapodia.

Ecology.—Endoparasitism among the Polychaetes is known to occur almost exclusively in members of the family Arabellidae. A review of the known endoparasitic arabellids (review by Pettibone 1957, Day 1960, Hartman & Fauchald 1971, Emerson 1974, Amaral 1977, Uebelacker 1978, Wu et al. 1982, San Martin & Sardá 1986) reveals that, with the exception of *Oligognathus bonelliae* Spengel, 1882 (found living within the body cavity of the Echiuroid *Bonellia viridis* Rolando), all the known arabellid parasites have been found within the body cavity or gut (in the case of *Haematocleptes terebellidis*) of polychaete hosts. *Pholadiphila turnerae* is unlike most of the parasitic arabellids in that it lives external to the host's body cavity (within its mantle cavity) and is the first arabellid reported to form an association with a mollusk.

It is not clear if the association between *P. turnerae* and the wood boring bivalves is commensal or parasitic. If the polychaete utilizes the host's mantle cavity simply as a refuge from predators (as Pettibone [1984] suggested may be true of the Polynoidae found in the mantle cavity of deep-water seep and vent mussels), then this would be an example of commensalism. There are several indications, however, that this association is actually a parasitic one. The mouthparts of *P. turnerae* are reduced in a similar manner to those of other arabellids known to be parasitic and argues for reliance upon a host for nutrition. Possible food sources within the pholad mantle cavity are the gill filaments, the mucus coat on these filaments, or perhaps partially digested material within the pholads wood storing caecum. The mere presence of such a large organism in the mantle cavity (Fig. 3A) may impede water flow to such an extent that a significant stress is placed upon the pholad host. If this is the case then this association must be considered a parasitic (parasite lives at the expense of its host) rather than a commensal (host is unaffected by the associated species) relationship.

Despite a large sampling effort in shallow waters, there have been few reports of polychaetes living as commensals or parasites within the mantle cavity of bivalve mollusks. A specimen of the syllid *Parasyllidea humesi* Pettibone, 1961 was reported from the mantle cavity of the intertidal bivalve *Tellina nymphalis* Lamark, however this must be considered as a fortuitous association because only one of the approximate 200 specimens of this polychaete collected by Pettibone (1961) was found within the bivalve, the remainder were free-living. The polychaete *Antonbruunia viridis* Hartman & Boss, 1965 (Family Antonbruunidae) has been described as a commensal in the mantle cavity of the bivalve *Lucina fosteri* Hartman & Boss, 1965 collected in 68–82.3 m off Madagascar. To date this is the only report of a polychaete species collected exclusively from the mantle cavity of a shallow water bivalve host.

With greater sampling effort in the deep sea close associations between polychaetes and bivalves are being noted with increasing frequency. Pettibone (1984, 1986) has described two species of Polynoidae living within the mantle cavity of mytilid mussels from both the Galapagos Rift hydrothermal vents and the Florida Escarpment methane seeps. Three species belonging to a recently described family, the Nautiliniellidae Miura & Laubier, 1989 (emended by Miura & Laubier [1990]), have been described from Japanese cold-seeps living within the mantle cavities of two species of *Calyptogenia* and a species of *Solemya.* Blake (1990) has also described a fourth species of Nautiliniellidae from the Laurentian Fan in the Western North Atlantic (3800–3900 m) living in the mantle cavity of *Thyasira insignis. Pholadiphila turnerae* is yet another example of a deep-sea polychaete which has taken up existence within a bivalve mantle cavity. The presence of commensal/parasitic polychaetes in the bivalve mantle cavity seems more common in the deep sea than in shallow water environments.

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THAUMATOCONCHA PIX, A NEW BATHYAL AND ABYSSAL SPECIES FROM OFF SE AUSTRALIA (OSTRACODA: HALOCYPRIDA: THAUMATOCYPRIDIDAE)

Louis S. Kornicker

Abstract.—*Thaumatoconcha pix* is described and illustrated from specimens collected at bathyal and abyssal depths (770–2900 m) from the continental slope off SE Australia. It is distinguished from previously described species by the morphology of the male copulatory organ. The genus has not been reported previously from the vicinity of Australia.

The family Thaumatocyprididae is of particular interest because of its unusual distribution (marine caves and the deep sea), which recently formed the basis for a hypothesis that the cave species are derived from shallow water habitats (Danielopol 1990), but the depths of the present occurrence (770–2900 m) does not add to or detract from that hypothesis. Members of the genus *Thaumatoconcha* have been collected at depths of from 150 to 4758 m between latitudes of about 32°N and 73°S in the Atlantic, Pacific, and Indian Oceans (Kornicker & Sohn 1976, Kornicker 1985), but none have been reported previously from the vicinity of Australia.

The specimens in this study are from collections made on the southeastern Australian continental slope during 1986 and 1988 by personnel of the Division of Natural History, Museum of Victoria, Victoria, Australia.

Disposition of specimens.—Three specimens have been deposited at the National Museum of Natural History, Smithsonian Institution, and have been assigned USNM numbers; remaining specimens have been deposited at the Museum of Victoria, Division of Natural History, Victoria, Australia, and assigned numbers.

Abbreviations.—The following abbreviations are used in the illustrations: am = central adductor muscle attachments; ant = antenna; bas = basale; BO = Bellonci organ; brn org = brown organ; co = copulatory organ; end = endopodite; esop = esophagus; ex = exopodite; fu = furca; gl = gland; hl = hinge line; lft = left; ll = lower lip; prot = protopodite; rt = right; ul = upper lip. Arabic numerals indicate limbs 1–7 as well as individual joints of each limb (the location of the numeral indicating whether a limb or joint is indicated). Roman numerals indicate the endites. Letters applied to bristles are standard in the literature. The following abbreviations are used in legends: lv = lateral view; mv = medial view.

Station Data

Slope 6. New South Wales, off Nowra (34°51.90′S, 151°12.60′E), 770 m, crinoid dominated, WHOI epibenthic sled, 15 Jul 1986.

Slope 7. New South Wales, off Nowra (34°52.29′S, 151°15.02′E), 1096 m, shell, WHOI epibenthic sled, 15 Jul 1986.

Slope 25. Victoria, south of Point Hicks (38°25.90′S, 148°58.60′E), 1850 m, muddy, sandstone, WHOI epibenthic sled, 22 Jul 1986.

Slope 27. Victoria, south of Point Hicks (38°25.00′S, 149°0.00′E), 1500 m, compacted clay, WHOI epibenthic sled, 22 Jul 1986.

Slope 32. Victoria, south of Point Hicks

(38°21.90′S, 149°20.00′E), 1000 m, WHOI epibenthic sled, 23 Jul 1986.

Slope 53. New South Wales, 54 km ESE of Nowra (34°52.72′S, 151°15.04′E), 996 m, mud, fine sand, fine shell, WHOI epibenthic sled, 22 Oct 1988.

Slope 66. Victoria, 96 km S of Point Hicks (38°40.29′S, 149°18.06′E), 2900 m, compacted clay, WHOI epibenthic sled, 25 Oct 1988.

Slope 69. Victoria, 76 km S of Point Hicks (38°29.33′S, 149°19.98′E), 1840 m, sandy mud, fine shell, WHOI epibenthic sled, 26 Oct 1988.

Slope 81. Tasmania, 48 km ENE of Cape Tourville (42°00.25′S, 148°43.55′E), 1264 m, gravel with lumps of sandy mud aggregate, WHOI epibenthic sled, 30 Oct 1988.

Order Halocyprida Dana, 1853
Suborder Halocypridina Dana, 1853
Superfamily Thaumatocypridoidea Müller, 1906
Family Thaumatocyprididae Müller, 1906

The Thaumatocyprididae include three living genera of which only *Thaumatoconcha* Kornicker & Sohn, 1976, is in the present collection. Classification is that proposed by Kornicker & Sohn (1976).

Genus *Thaumatoconcha* Kornicker & Sohn, 1976

Type species.—*Thaumatoconcha radiata* Kornicker & Sohn, 1976:35.

Composition.—Nine species are known in this genus including a new species described herein; in addition, several previous records have been left in open nomenclature (Kornicker 1985).

Distribution.—Between 32°N and 73°S at depths of 150–4758 m (Kornicker & Iliffe 1989:fig. 1).

Thaumatoconcha pix, new species
Figs. 1–3a–f

Etymology—From the Latin *pix* (pitch).

Holotype.—Adult male with body separated from shell in alcohol, in collection of the Museum of Victoria (J24007).

Type locality.—Slope 27, 38°25.00′S, 149°00.00′E: depth 1500 m.

Paratypes.—Slope 6, 2 undissected juveniles in alcohol (largest specimen: length 1.39 mm, height 1.13 mm). Slope 7, 1 specimen in alcohol. Slope 25, 2 specimens in alcohol. Slope 27, USNM 193894, adult male in alcohol and on slide (copulatory organ); USNM 193893, 1 adult male in alcohol and on slide; USNM 193895, 1 adult female in alcohol and on slide; 18 specimens in alcohol. Slope 32, 1 specimen in alcohol. Slope 53, 1 adult male and a total of 7 adult females and juveniles, all in alcohol. Slope 66, 4 specimens in alcohol. Slope 69, 68 specimens in alcohol. Slope 81, 5 specimens in alcohol (J24008–J24017).

Distribution.—Off SE Australia; known depth range 770–2900 m.

Remarks.—Because the carapace and most appendages of the new species are similar to those of the type species *T. radiata,* they are compared to that species in the description.

Description of adult male (Figs. 1–3a, b).—Carapace similar in shape and ornamentation to that of *T. radiata* (Fig. 1a). Free margin with numerous pore canals perpendicular to valve edge. Surface with widely separated slender bristles, many branching distally.

Central adductor muscle attachments (Figs. 1a, b, 3b): Typical for genus.

Carapace size (length, height in mm): Slope 27: holotype, 1.94, 1.66. Slope 25: USNM 193893, 1.97, 1.58.

First antenna (Fig. 1c–e): With 8 well-defined joints. 1st joint with medial spines and 2 spinous bristles (1 dorsal, 1 lateral oriented backwards). 2nd joint with medial spines and 2 spinous bristles (1 distoventral, 1 dorsal). 3rd joint with medial, ventral, and dorsal spines. 4th joint with dorsal spines and 2 long ventral bristles with distal widely separated minute spines. 5th joint with few minute dorsal spines and 3 ventral bristles (longest and stoutest with abundant long

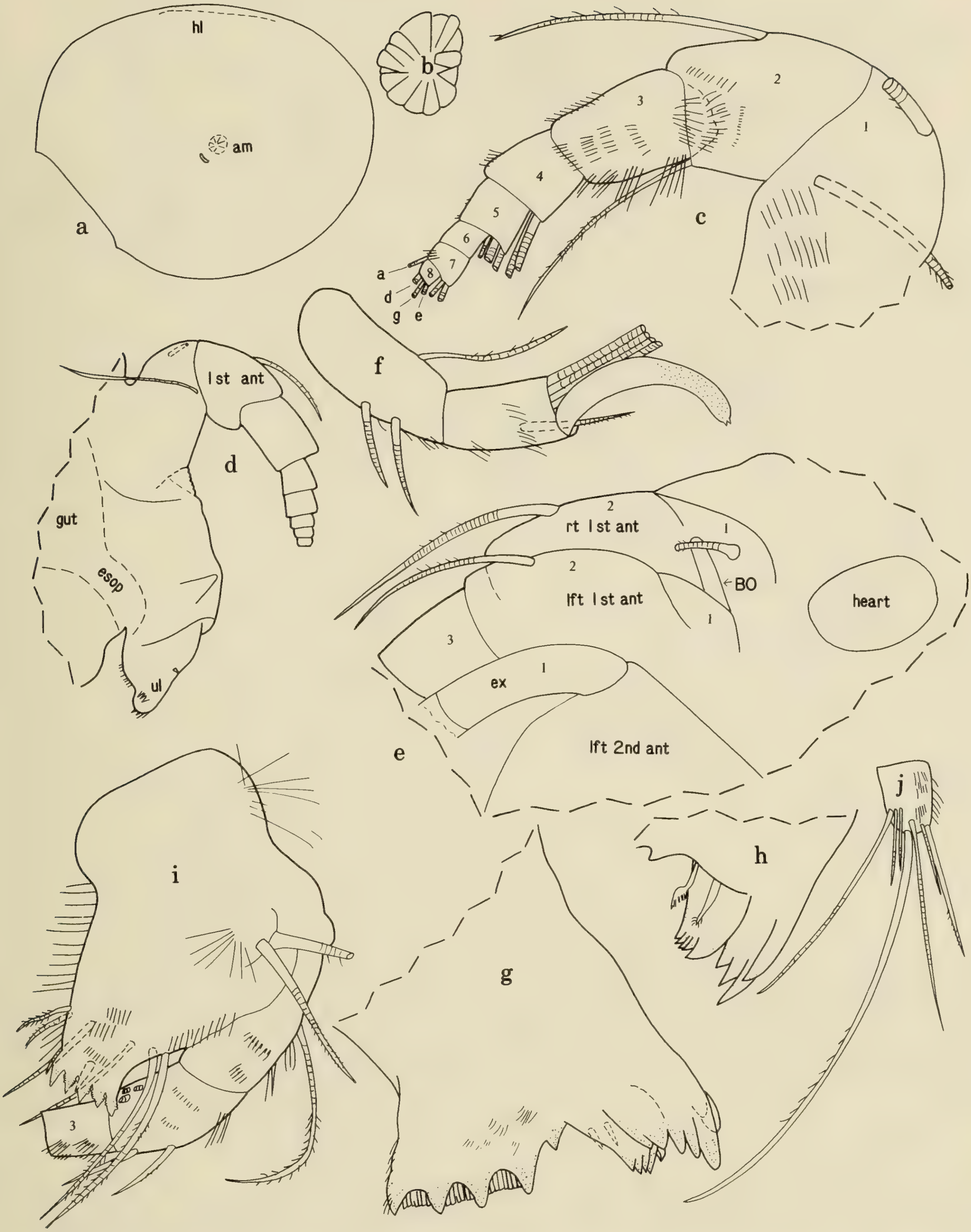

Fig. 1 *Thaumatoconcha pix,* adult male, paratype, USNM 193893: a, Complete specimen from left side, anterior to left, length 1.97 mm; b, Detail of central adductor muscles shown in "a"; c, Right 1st antenna, mv; d, Anterior part of body from right side (not all appendages shown); e, Anterodorsal part of body from left side; f, Endopodite of right 2nd antenna, mv; g, Distal end of coxale endite of right mandible, lv; h, Anterodistal corner of coxale endite of left mandible, mv; i, Basale and endopodite of left mandible (not all bristles of endopodite shown), mv; j, 3rd endopodial joint of left mandible, mv.

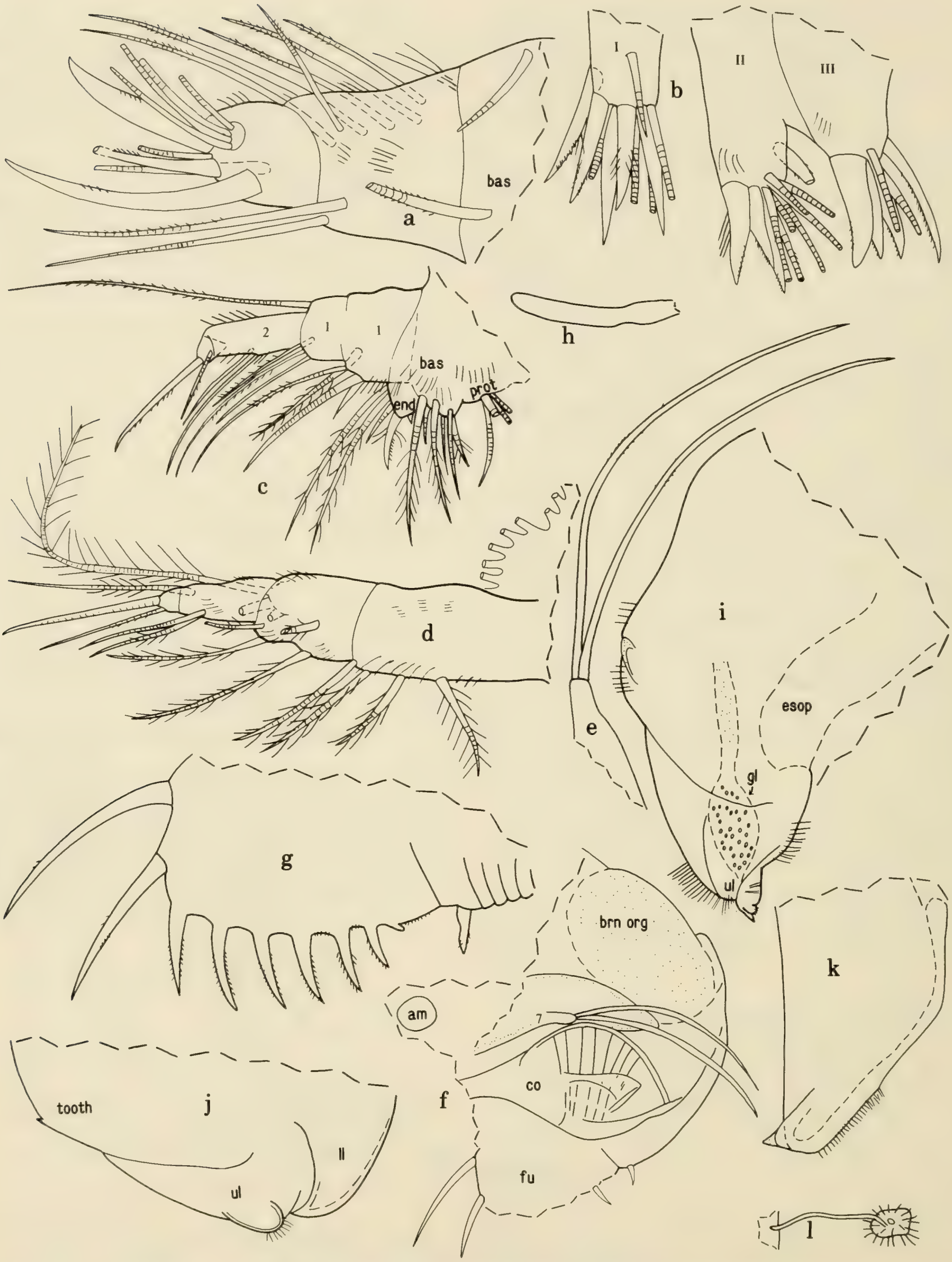

Fig. 2. *Thaumatoconcha pix,* adult male, paratype, USNM 193893: a, Maxilla (endites not shown); b, Endites of maxilla; c, 5th limb (epipodite not shown); d, 6th limb (only distal part of epipodite shown); e, Left 7th limb; f, Posterior of body from left side (not all appendages, furcal claws, or distal end of copulatory organ shown); g, Left lamella of furca; h, Bellonci organ; i, Anterior of body from left side (not all appendages shown); j, Upper and lower lips from left side; k, Lower lip from left side; l, Protistan attached to maxilla.

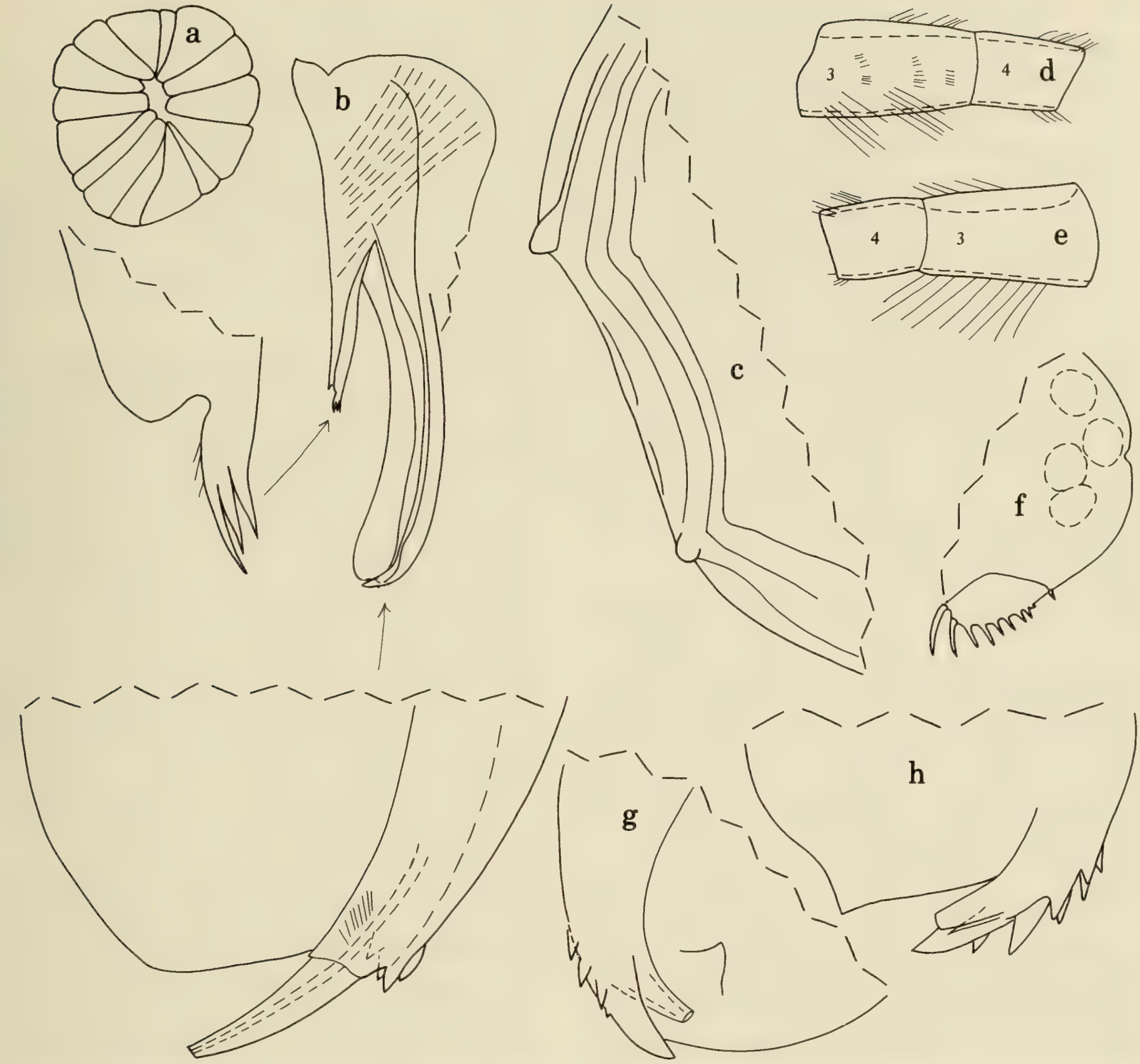

Fig. 3. *Thaumatoconcha pix,* adult male, paratype, USNM 193894, length 1.94 mm: a, Central adductor muscle attachments of left valve, lv; b, Copulatory organ with details of tips of anterior and posterior branches, anterior to right, mv. Adult female, paratype, USNM 193895, length 1.97 mm: c, Anterior of left valve, lv; d, e, joints 3 and 4 of left (mv and lv) 1st antenna; f, Posterior of body from left side showing unextruded eggs (dashed) and left furcal lamella. *Thaumatoconcha radiata* Kornicker & Sohn, 1976, adult male, paratypes, tip of anterior branch of copulatory organ: g, USNM 143753C, anterior to left (South Atlantic, 2707 m); h, USNM 126136E, anterior to left (Weddell Sea, 3035 m).

distal ventral hairs; next size with distal widely spaced minute spines; shortest with few minute spines). 6th joint bare. 7th joint with few indistinct medial spines, 1 short dorsal spinous a-bristle and 2 ventral bristles (b- and c-bristles; latter longer) with distal widely separated minute spines. 8th joint with short spinous dorsal bristle (base lateral (d-bristle)) and 2 longer ventral bristles with widely separated minute spines (lateral much longer (e-bristle), other g-bristle).

Second antenna (Fig. 1e, f): Protopodite with rows of long spines along ventral margin. Endopodite 3-jointed (Fig. 1f): 1st joint with ventral spines and 3 bristles (1 dorsal, 2 ventral); 2nd joint with ventral and medial spines and 4 long terminal bristles near dorsal margin and 1 short spinous lateral bristle near ventral margin; 3rd joint forming stout sclerotized hook with minute distal pustules and 2 minute terminal teeth. Exopodite with 9 joints; 1st joint with suture dividing it into long proximal and short distal parts; joints 2–8 with long bristles with natatory hairs and some also with slender ventral spines; 9th joint with 2 bristles (1 long with slender ventral spines and distal natatory hairs, 1 short with slender ventral and dorsal spines).

Mandible: Coxale endite with proximal and distal sets of teeth separated by small space with single low triangular tooth (Fig. 1g): proximal set with 4 teeth (proximal tooth with 1 pointed cusp, following teeth with 3, 4 and 3 cusps) with dense bundles of spines between teeth (spines also on medial and lateral surfaces proximal to teeth); distal set with 2 flat teeth (inner set with 5 or 6 cusps; outer set with 6 cusps) with 2 bristles (with spinous tips) at base (Fig. 1h). Basale (Fig. 1i): distal edge with 5 triangular cusps (anterior 4 with minute marginal serrations on proximal ⅔); posterior margin of endite with long hairs and 2 bristles (proximal spinous, distal bare, tubular); anterior margin of endite with long spinous bristle; lateral side of endite with long hairs, 4 spinous bristles, and distal stout bare triangular tooth; medial side of basale near dorsal edge with 2 stout bristles on small mound. Endopodite 3-jointed (Fig. 1i): 1st joint spinous, with spinous dorsal bristle; 2nd joint spinous, with 3 ventral bristles and 2 distal dorsal bristles; 3rd joint hirsute with 7 bristles (Fig. 1j).

Maxilla (Fig. 2a, b): Endite I with 10 bristles; endite II with 11 bristles; endite III with 6 bristles (Fig. 2b). Basale with 2 bristles. 1st endopodial joint with 5 or 6 dorsal bristles and 2 ventral. 2nd endopodial joint with 9 bristles.

Fifth limb (Fig. 2c): Epipodite with bristles in 3 groups, each with 4 (distal group) or 5 bristles (not shown). Protopodite, basale, and endopodite with total of about 17 bristles including small tooth-like process on endopodite (some protopodial bristles missing from drawing of illustrated limb). Exopodite 3-jointed: 1st joint with broad proximal part (with 4 bristles near ventral margin) and narrower distal part (with 3 bristles near ventral margin and 1 long dorsal bristle); 2nd joint with 2 bristles on or near ventral margin at midlength; 3rd joint with 1 short bristle and 1 long claw-like bristle (short bristle 42–57% length of long bristle).

Sixth limb (Fig. 2d): Epipodite with bristles in 3 groups (4 bristles in middle group, 5 bristles in distal group, proximal group fragmented; not all bristles shown). Protopodite with 4 hirsute bristles on or near ventral margin. Basale fused to 1st exopodial joint, with 2 hirsute bristles. Endopodite a small process with 3 long plumose bristles. Exopodite: 1st joint with 2 hirsute bristles; 2nd joint with 3 bristles (1 dorsal, 2 ventral); 3rd joint with 1 short bristle and 1 long claw-like bristle (short bristle 83–88% length of long bristle).

Seventh limb (Fig. 2e, f): Small with 2 long apical bristles.

Furca (Fig. 2f, g): Each lamella with 2 long articulated anterior claws followed by 6 short nonarticulated claws and 1 short recurved nonarticulated process. Most claws with indistinct minute teeth along margins (not all shown in illustrated furca). Neither lamella anterior to other.

Bellonci organ (Figs. 1e, 2h): Elongate with rounded tip.

Eyes: Absent.

Lips: Upper lip similar to that of *T. radiata* (Figs. 1d, 2i, j). Lower lip a triangular process at each side of mouth (Fig. 2j, k).

Anterior of body (Figs. 1d, 2i, j): Small sclerotized anterior tooth on each side of body dorsal to upper lip (stippled in Fig. 2i, j).

Posterior of body (Fig. 2f, g): Single slender tooth-like process present proximal to furcal lamellae. Posterior of body divided into narrow annulations (Fig. 2g).

Copulatory organ (Figs. 2f, 3b): Single organ on left side of body consisting of 2 parts:

tip of anterior part with single large toothlike process with several small teeth at base; posterior part shorter than anterior part, with 3 teeth at tip.

Protistans: USNM 193893 with long-stalked protistans on 1st antennae, mandibles, and maxillae (Fig. 21).

Description of adult female (Fig. 3c–f).— Carapace similar to that of adult male (Fig. 3c).

Carapace size (length, height in mm): USNM 193895, 1.97, 1.78.

First antenna: Similar to that of female *T. radiata* except weak suture present between 3rd and 4th joints (Fig. 3d, e).

Second antenna: Limb similar to that of female *T. radiata.* 9th exopodial joint with 2 bristles (USNM 193893, left limb).

Furca (Fig. 3f): Similar to that of adult male. USNM 193893 with left lamella slightly anterior to right. Remaining appendages not examined in detail.

Eggs: USNM 193893 with 5 or 6 unextruded eggs (only 4 shown in Fig. 3f).

Comparisons.—In the known species of the genus, only *T. radiata* and *T. pix* have more than 1 or 2 teeth at the tip of the anterior part of the male copulatory organ. The 2 species differ in that the organ of *T. radiata* has 2 large terminal teeth whereas that of *T. pix* has only 1 (compare Fig. 3b, g, h).

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A NEW SPECIES OF *ANTHESSIUS* (COPEPODA: POECILOSTOMATOIDA) ASSOCIATED WITH *BERTHELLA STELLATA* (RISSO, 1826) (GASTROPODA: OPISTHOBRANCHIA)

P. J. López-González, M. Conradi, S. Naranjo, and
J. C. García-Gómez

Abstract.—Only four species of the genus *Anthessius* Della Valle, 1880 are known to be associated with notaspidean molluscs. Only *A. pleurobrancheae* Della Valle, 1880 has been reported in European waters, and has not been seen since the original description. In this paper, *A. arcuatus,* associated with *Berthella stellata* (Risso, 1826) from Spanish waters, is described and compared with other congeneric species associated with notaspidean molluscs. The diagnostic characters of this species are the second maxilla, the labrum, and leg 5.

The fauna of copepods associated with invertebrates is relatively unknown in the Iberian Peninsula. Although the majority of this fauna is probably scientifically known and reported from the European and North African coasts, it is likely that, during the next few years, new species will be described from material obtained in the Iberian Peninsula.

During the Marine Biology Expedition "Bahía'90" in Algeciras Bay (Cádiz, Spain), some specimens of the genus *Anthessius* were collected from the gills of four specimens of the notaspidean *Berthella stellata* (Risso, 1826).

A close examination of these copepods revealed that they do not correspond to Della Valle's (1880) *Anthessius pleurobrancheae.* In the course of studying this species, several synapomorphies were discovered in the species of *Anthessius* that are normally associated with sea slugs of the Order Notaspidea. Therefore, a discussion on this matter will be given following the description of the new species.

Materials and Methods

The opisthobranch molluscs were collected under stones from intertidal and upper infralittoral zones. These specimens were maintained in separate glass bottles. The copepods were taken from the gills and pallial cavity of sea slugs and were preserved in a solution of ethyl alcohol (70% in seawater). The specimens were dissected under a stereomicroscope and semipermanent mounts were made using CMC 10 and lignin pink. All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

Family Anthessiidae Humes, 1985
Genus *Anthessius* Della Valle, 1880
Anthessius arcuatus, new species
Figs. 1–4

Type material.—4 ♀♀, 2 ♂♂ and 3 copepodites from the gills of 4 specimens of the opisthobranch mollusc *Berthella stellata* (Risso, 1826) in El Campamento (San Roque), Algeciras Bay, Cádiz, Spain, 7 Jul 1990.

Female.—Body (Fig. 1a, b) cyclopiform, length (not including setae on caudal rami) 1.79 mm (1.75–1.82 mm) and greatest width 1.01 mm (1.00–1.02 mm) based on 4 specimens in 70% ethyl alcohol. Ratio of length to width of prosome 0.72:1. Ratio of length

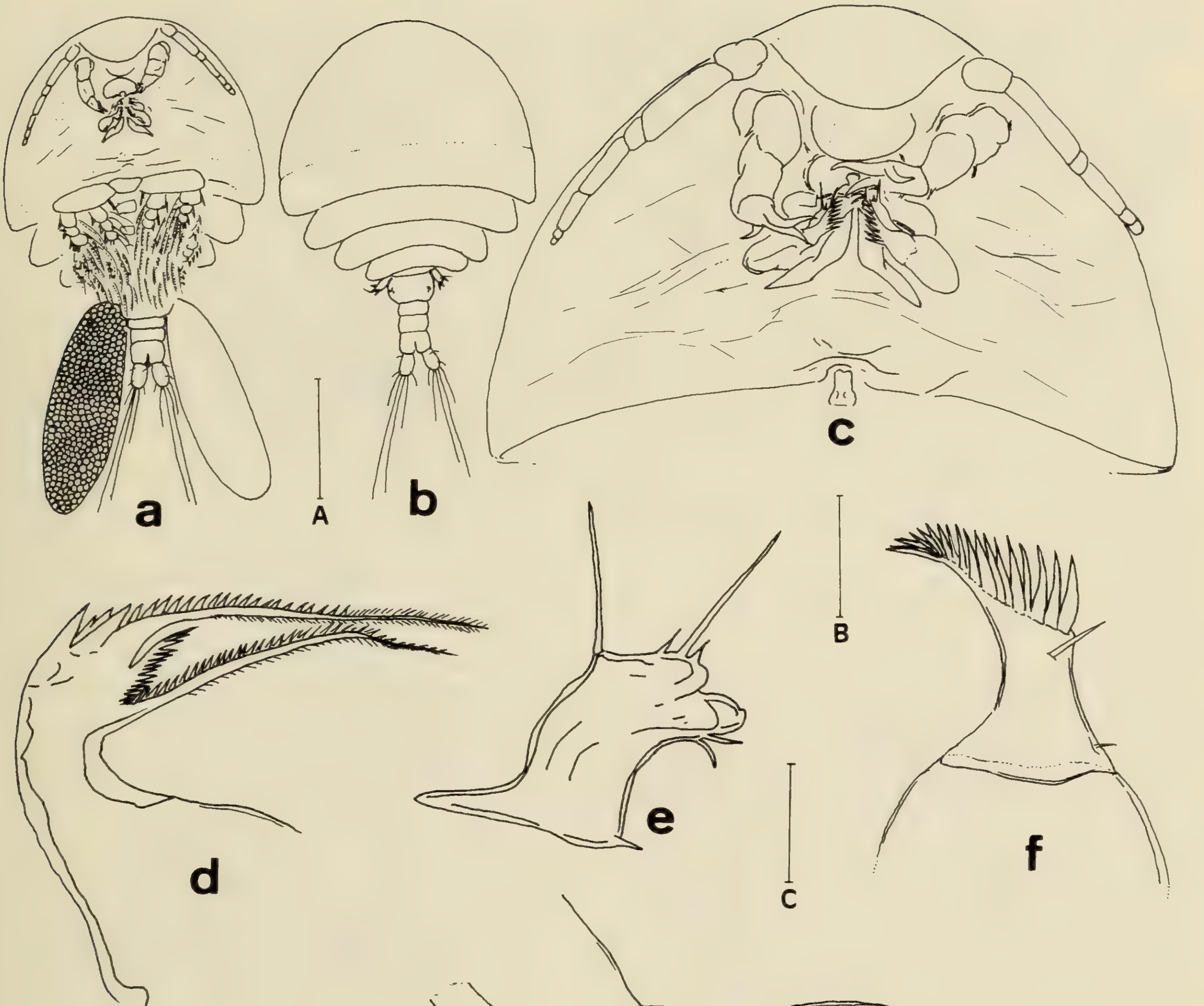

Fig. 1. *Anthessius arcuatus,* new species. Female: a, ventral (A); b, dorsal (A); c, cephalotorax, ventral (B); d, mandible (C); e, first maxilla (C); f, second maxilla (C); g, maxilliped (C); h, labrum and paragnaths, ventral (C); i, tip of second antenna, posterior (D); j, second antenna (C). Scale: A, 550 μm; B, 170 μm; C, 50 μm; D, 100 μm.

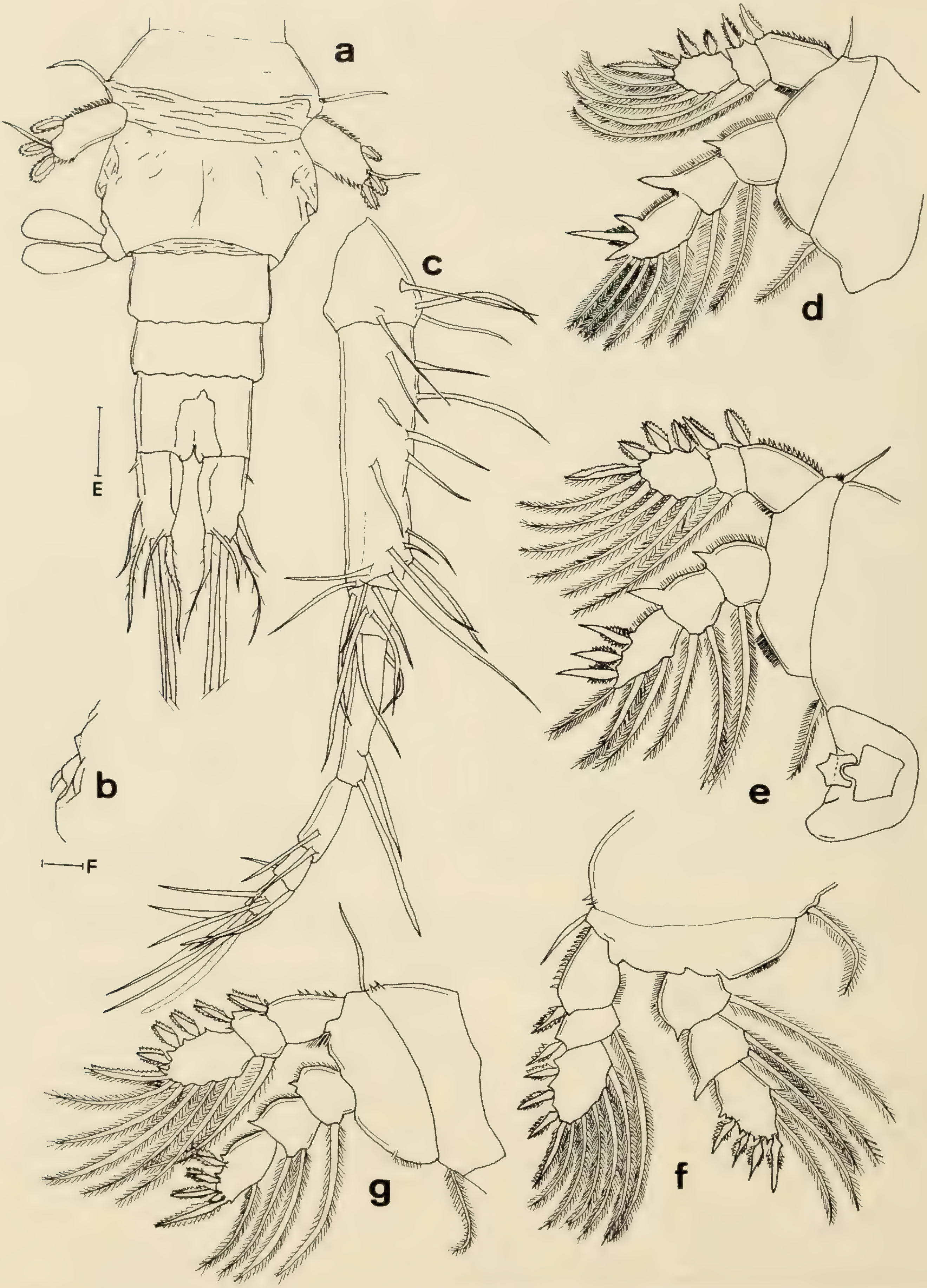

Fig. 2. *Anthessius arcuatus,* new species. Female: a, urosome, dorsal (E); b, egg sac, attachement area, dorsal (F); c, first antenna, dorsal (D); d, leg 1, anterior (D); e, leg 2 and intercoxal plate, anterior (D); f, leg 3, anterior (D); g, leg 4, anterior (D). Scale: E, 100 μm; F, 12 μm.

of prosome to that of urosome 1.43:1. Segment of leg 1 separated dorsally from head by transverse furrow. Segment of leg 5 (Fig. 2a) 300 × 150 μm. Genital segment wider than longer, 160 × 300 μm; mid-region with dorsal longitudinal suture about three-fourths length of genital segment (Fig. 2a). Genital areas located dorsolaterally, just posterior to widest part of segment. Each area (Fig. 2b) without seta, with a small spiniform process about 3 μm long. Two postgenital segments from anterior to posterior 90 × 200 μm, 70 × 180 μm, and the anal segment 110 × 160 μm. Caudal ramus 115 × 60 μm, 2× longer than wide bearing 6 setae. One anterior lateral setule is 3 μm and naked. Outer posterior lateral seta 150 μm and naked, dorsal seta 70 μm and naked, outermost terminal seta 180 μm, innermost terminal seta 200 μm, and the two long median terminal setae 440 μm (outer) and 730 μm (inner). Medial margin caudal ramus convex.

Egg sac elongate, 1.25 × 0.38 mm, extending beyond tips of longest ramal setae, and containing numerous eggs, each about 50 μm in diameter.

Rostrum (Fig. 1c) rounded posteroventrally.

First antenna (Fig. 2c) about 444 μm long. Lengths of 7 segments (measured along their posterior non-setiferous margins): 20 (90 μm along anterior margin) 175, 32, 105, 52, 30 and 30 μm; respectively. Formula for armature 4, 15, 4, 4, 2, 2 and 7 + 1 aesthetes. All setae naked.

Second antenna (Fig. 1j, i) 3-segmented. Formula for armature: 1, 1, and 6 + 1 setule + two claws + one claw-like process. Third segment, 100 μm along its outer edge, 90 μm along its inner edge and 90 μm wide, bearing 3 short setae on inner side, 3 long setae on outer side, 2 claws (100 and 89 μm, respectively) and a claw-like process 35 μm. All elements naked.

Labrum (Fig. 1h) with 2 broad posteroventral lobes, separated by a deep arch, with pair of digitiform processes medially; posterior edge of lobes and the inner edge of the arch denticulated. Paragnates presents, denticulated.

Table 1.—Armature of legs. (Roman numerals = spines; Arabic numerals = setae; exp = exopod; end = endopod.)

	Leg	Coxa	Basis	Armature
♀♀	1st	0–1	1–0	exp: I–0; I–1; III,I,4 end: 0–1; 0–1; I,5
	2nd	0–1	1–0	exp: I–0; I–1; III,I,5 end: 0–1; 0–2; III,3
	3rd	0–1	1–0	exp: I–0; I–1; III,I,5 end: 0–1; 0–2; IV,2
	4th	0–1	1–0	exp: I–0; I–1; III,I,5 end: 0–1; 0–2; IV,1
♂♂	1st	0–1	1–0	exp: I–0; I–1; III,I,4 end: 0–1; 0–1; II,4

Mandibule (Fig. 1d) with concave side having an incision, followed by two long prominent spinulose lashes; between these, a denticulate process; convex with strong denticles. First maxilla (Fig. 1e) bilobed, with outer lobe bearing 2 long setae, each 65 μm and 2 short setae, each 10 μm; inner lobe with only 2 setae, 60 and 62 μm. All elements naked. Second maxilla (Fig. 1f), 2-segmented; first segment unornamented; second segment bearing denticulated lash, with small setule on its proximal outer surface and posterior seta. Maxilliped (Fig. 1g) 3-segmented, greatly reduced, the pointed distal segment bears a small subterminal seta.

Area between maxilliped and first pair of legs with well-defined line, slightly protuberant.

Legs 1–4 (Fig. 2d–g) with 3-segmented rami. Formula for armature in Table 1.

Inner coxal setae are pinnate. Row of spinules on lateral margin of first exopodal segment of legs 1–4. Inner margin of basis of legs 1–4 with row of spinules.

Leg 5 (Fig. 2a) with free segment, 115 × 50 μm, with anterior and posterior borders denticulated, and carrying 3 serrated spines and 1 naked dorsal seta. Segment of leg 5 with a naked seta, 90 μm long.

Male.—Body very similar to that of female (Fig. 3a, b). Length (excluding setae on caudal rami) 1.33 mm and greatest width 0.69 mm, based on 2 specimens in 70% ethyl alcohol. Ratio of length to width of prosome 0.64:1. Ratio of length of prosome to that of urosome 1.13:1.

Segment of leg 5 (Fig. 4a) 100 × 210 μm. Four postgenital segments from anterior to posterior 50 × 160 μm, 60 × 140 μm, 40 × 135 μm and 70 × 125 μm (Fig. 4a).

Caudal ramus resembling that of female, 95 × 55 μm, with ratio 1.72:1 (Fig. 4c).

Rostrum rounded posteroventrally. First antenna (Fig. 3i) similar to that of female, but three additional aesthetes on second segment, resulting in formula of 4, 15 + 2 aesthetes, 4 + 1 aesthete, 4, 2, 2 and 7 + 1 aesthete.

The second antenna (Fig. 3j) is similar to that of female, but inner side of third segment bearing 4 short setae, 3 long setae on outer side, 2 claws, and a claw-like process. All elements naked.

Labrum, mandible, paragnaths, first maxilla and second maxilla (Fig. 3c–f) like those of female. Maxilliped (Fig. 3g, h) 4-segmented; first segment bearing a setose area near union with second segment; second segment with 2 long setae, 3–7 rows of spines on inner side and 3 short spinules near insertion of third segment, which has 2 setae; claw 200 μm with concave edge denticulate and short seta.

Legs 1–4 (Fig. 4e–i) with similar spinal and setal formula as in female, except third segment of endopod of leg 1 (Fig. 4f) (formula in Table 1).

Leg 5 (Fig. 4b) free segment 105 × 50 μm, similar to that of female.

Leg 6 (Fig. 4d) consisting of posteroventral flap on genital segment and bearing 2 naked setae, 45 μm and 30 μm, and spiniform process.

Spermatophore 120 × 50 μm.

Sexual dimorphism.—The spines of the third endopod segment of all the legs are different in each sex. These spines are acutely lanceolate and denticulate in their proximal half in the female, but in the male they are large, more blunt and slightly denticulate along the entire length.

Etymology.—The specific name *arcuatus,* from Latin *arcuatus* = arch shaped, alludes to the characteristic posterior region of the labrum. The holotype has been deposited in the Museo Nacional de Ciencias Naturales de Madrid (Spain) (MNCNM 20.04/2722).

Discussion

The genus *Anthessius* has been included in various families since its original description by Della Valle (1880) e.g., Lichomolgidae (Stock 1959, Humes & Ho 1965, Humes 1973) and Myicolidae in Stock et al. (1963) following the opinion of Illg (1960). The latter designation has been accepted by other authors (Humes & Stock 1965; Humes 1973, 1976; Ho 1983). Recently, Humes (1985) created the family Anthessidae with *Anthessius* as type genus, with four other genera, *Katanthessius, Neanthessius, Panaietis* and *Rhinomolgus.*

Of all species belonging to *Anthessius* associated with notaspidean molluscs, only *A. pleurobrancheae* Della Valle, 1880 was known in European waters. This species was collected on *Pleurobranchaea* sp. in Napoles, and was never reported again.

Ho (1983) recognized two different groups among the 34 species of the genus *Anthessius*: one group is found in pelecypods and the other associated with notaspidean sea slugs. The members of the latter group have five features in common: 1) a second antenna armed with three terminal spines; 2) a mandible bearing a short dentate lamella between the bases of the apical lash and the setiform element; 3) a second maxilla armed with a large number of teeth (at least ten) in the terminal process; 4) the last segment of leg 4 exopod having a formula of III, I, 5; and 5) the endopods of legs 2 through 4

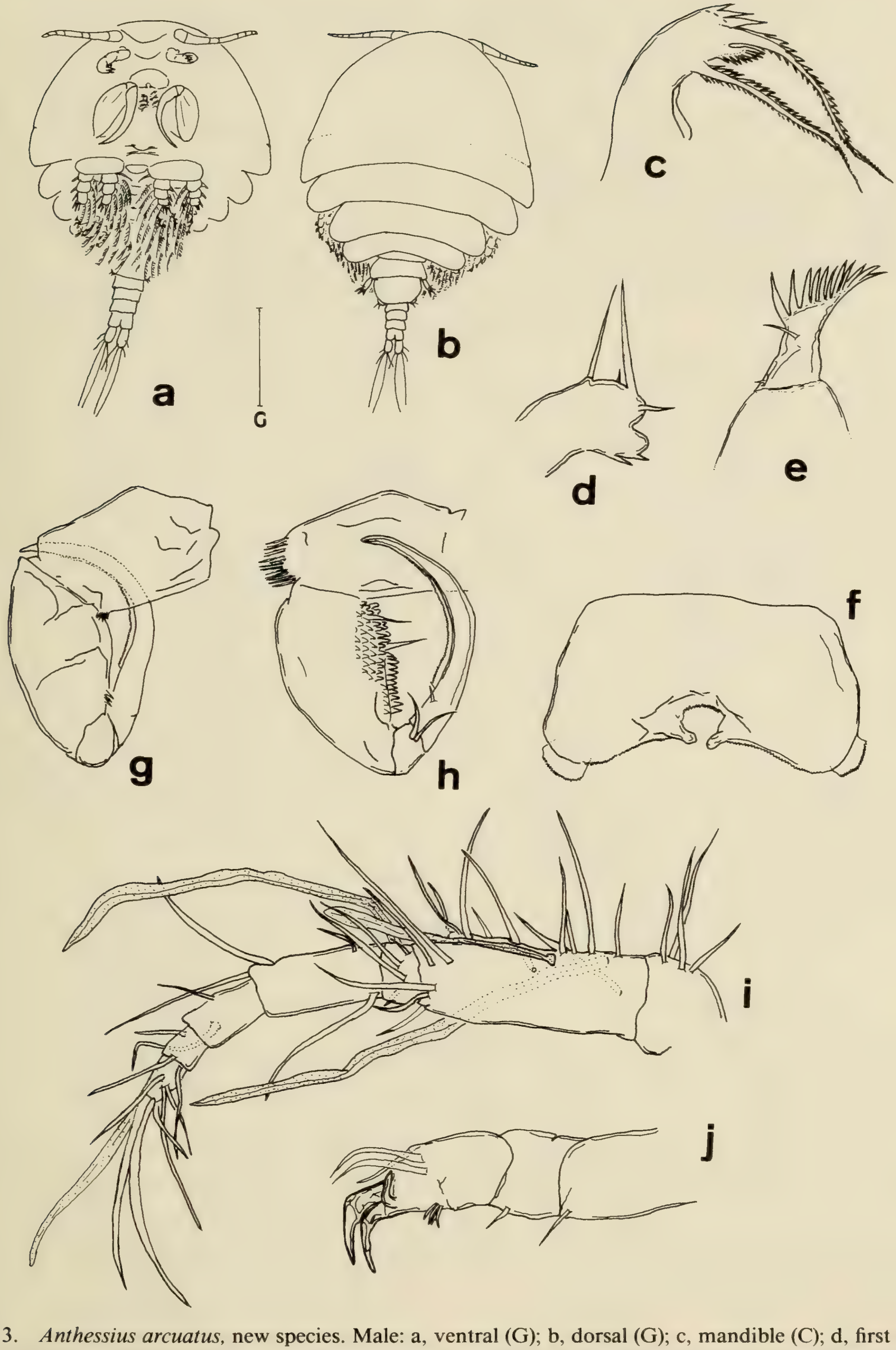

Fig. 3. *Anthessius arcuatus,* new species. Male: a, ventral (G); b, dorsal (G); c, mandible (C); d, first maxilla (C); e, second maxilla (C); f, labrum and paragnaths, ventral (C); g, maxilliped, outer; h, maxilliped, inner; i, first antenna, dorsal (D); j, second antenna, posterior (D). Scale: G, 420 μm.

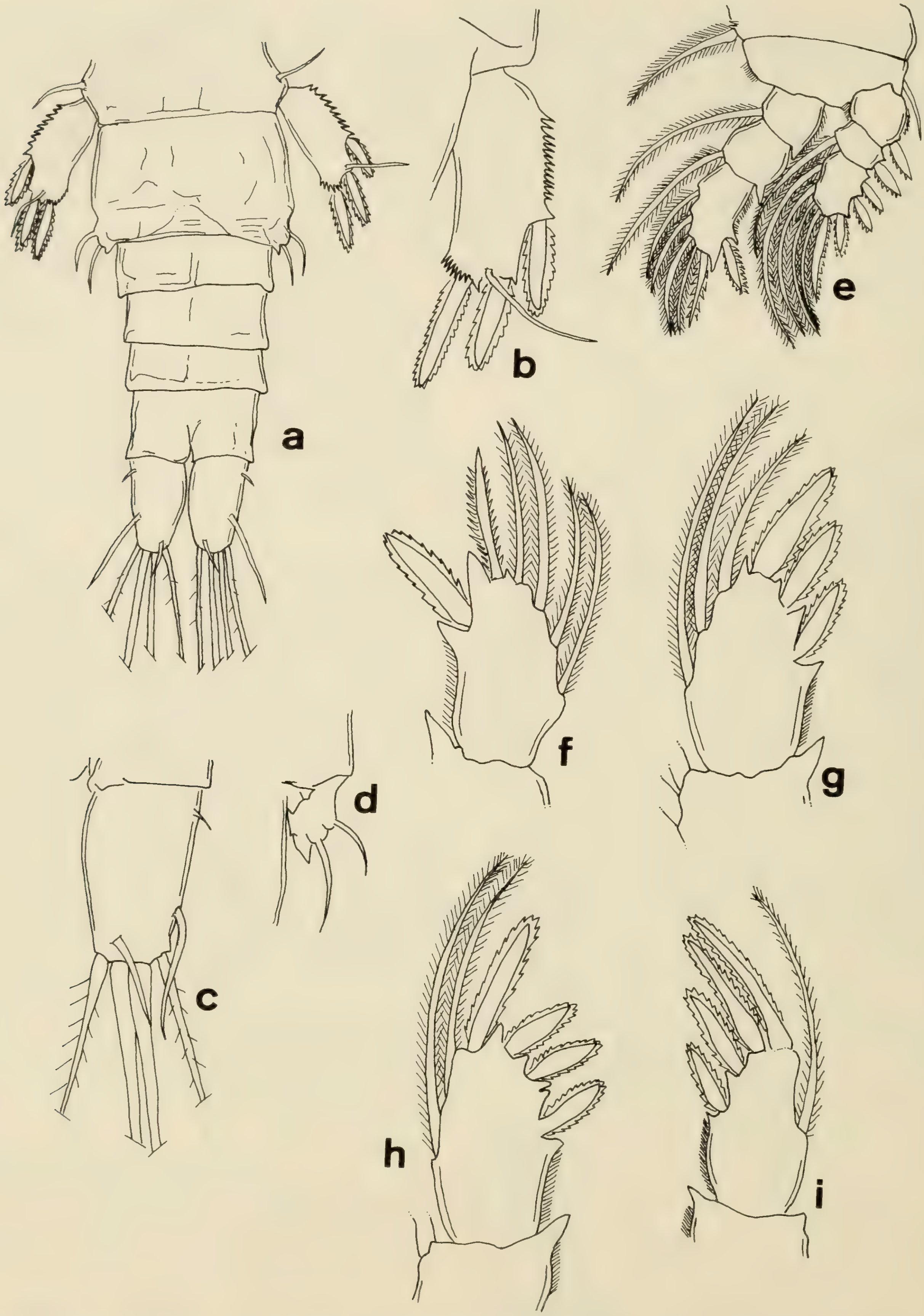

Fig. 4. *Anthessius arcuatus,* new species. Male: a, urosome, dorsal (E); b, leg 5, dorsal (C); c, caudal ramus, dorsal (C); d, leg 6, ventral (C); e, leg 1, ventral (D); f, terminal endopodal segment of leg 1 (C); g, terminal endopodal segment of leg 2 (C); h, terminal endopodal segment of leg 3 (C); i, terminal endopodal segment of leg 4 (C).

in the male bearing obtuse and smooth (instead of pointed and denticulate) spines (Ho 1983). *A. arcuatus* also has these five characteristics.

The *Anthessius* associated with notaspidean are: *A. pleurobrancheae* Della Valle, 1880, *A. hawaiiensis* (Wilson, 1921), *A. ovalipes* Stock et al. 1963 and *A. obtusispina* Ho, 1983. The most important difference among these species and *A. arcuatus* are the form of the two posteroventral lobes of the labrum. Furthermore, *A. ovalipes* has a prominent and well-defined postoral protuberance that our species does not have. *A. obtusispina* is very different, i.e., the mandible has a short dentate lamella between the apical lash and the long setiform element, the inner lobe of the first maxilla bears only one short, stubby element, the pointed distal segment of the maxilliped of the female bears a small subterminal seta, and leg 5 is armed with 3 slender setiform spines. The second maxilla of *A. hawaiiensis* has a low apical sclerotized portion, not inclining anteriorly in a marked angle to the remainder of the appendage while this appendage in *A. arcuatus* has an apical portion sharply angled and ornamented with strong denticles. The proximal outer spine of the third endopodal segment of the second leg and the spines of the third endopodal segment of leg 4 of the male in *A. concinnus* are smooth and obtuse. These spines in *A. arcuatus* are denticulated. Also, *A. concinnus* (female: 2.90 mm long; Stock et al. 1963) is larger than *A. arcuatus* (female: 1.78 mm long).

Anthessius pleurobrancheae is the species that is geographically closest to the type locality of the new species. Although the original description of Della Valle (1880) is poor there are some apparent differences to *A. arcuatus.* These features are the absence of spines in leg 5: "Il piede del quinto paio sono piú allungati dell altro *Anthessius* (Referred to *Anthessius solenocurti* Della Valle, 1880), e muniti non de spine, ma di setole" (Della Valle 1880:58); the ratio of the length to the width of leg 5 is higher in *A. pleurobrancheae* (2.75:1) than in *A. arcuatus* (2.3:1).

Detailed examination of new specimens of *Anthessius* collected in Napoles (the type-locality) will permit clarification of the taxonomic status of *Anthessius pleurobrancheae* as well as establishing differences among its congeners, associated with notaspideans.

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We thank Dr. A. G. Humes (Woods Hole, Massachusetts), Dr. J. H. Stock (Amsterdam) and Dr. R. V. Gotto (Belfast, Northern Ireland) for generous help with information and literature, and Dr. J-S. Ho (Long Beach, California) for revising the first draft of this manuscript and for valuable suggestions. We are grateful to Dr. L. Cervera for help during this project.

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CYCLOPOID AND HARPACTICOID COPEPODS (CRUSTACEA) FROM SOUTHEASTERN ALASKA, U.S.A.

Teruo Ishida

Abstract.—Species of cyclopoid and harpacticoid copepods from a marsh by the Montana River, Juneau, S.E. Alaska, U.S.A. included *Diacyclops languidus, Speocyclops yezoensis, Gulcamptus uenoi* and *Bryocamptus hiatus.* The genera *Speocyclops* and *Gulcamptus* are recorded for the first time from the Nearctic. *Bryocamptus hiatus* deviates from populations of eastern North America in the number of setae of legs 2–5.

I was given a sample of detritus collected with a fine mesh hand net from a marsh by the Montana River, Juneau, S.E. Alaska (58°29'N, 134°37'W) on 15 October 1984, by Dr. M. Saneyoshi of Hokkaido University, who visited there to study salmonid fishes. The sample contained six species of Copepoda: *Diacyclops languidus* (Sars, 1863), 1 ♀; *Speocyclops yezoensis* Ito, 1954, 2 ♂♂; *Maraenobiotus brucei* (Richard, 1898), 30+ ♀♀, 15+ ♂♂; *Gulcamptus uenoi* Miura, 1969, 9 ♀♀; *Epactophanes richardi* Mrazek, 1893, 1 ♀; *Bryocamptus hiatus* (Willey, 1925), 110+ ♀♀; 90+ ♂♂. These species, except *Maraenobiotus brucei* and *Epactophanes richardi,* are either poorly known or new distribution records. The purpose of this paper is to note and illustrate these species.

Whole and/or dissected specimens were mounted on permanent slides in gum-chloral medium. Examination and drawings were made principally from the permanent slides. The specimens were deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Diacyclops languidus (Sars, 1863)
Figs. 1–2

Material examined.—1 ♀, dissected on 1 slide: USNM 251162.

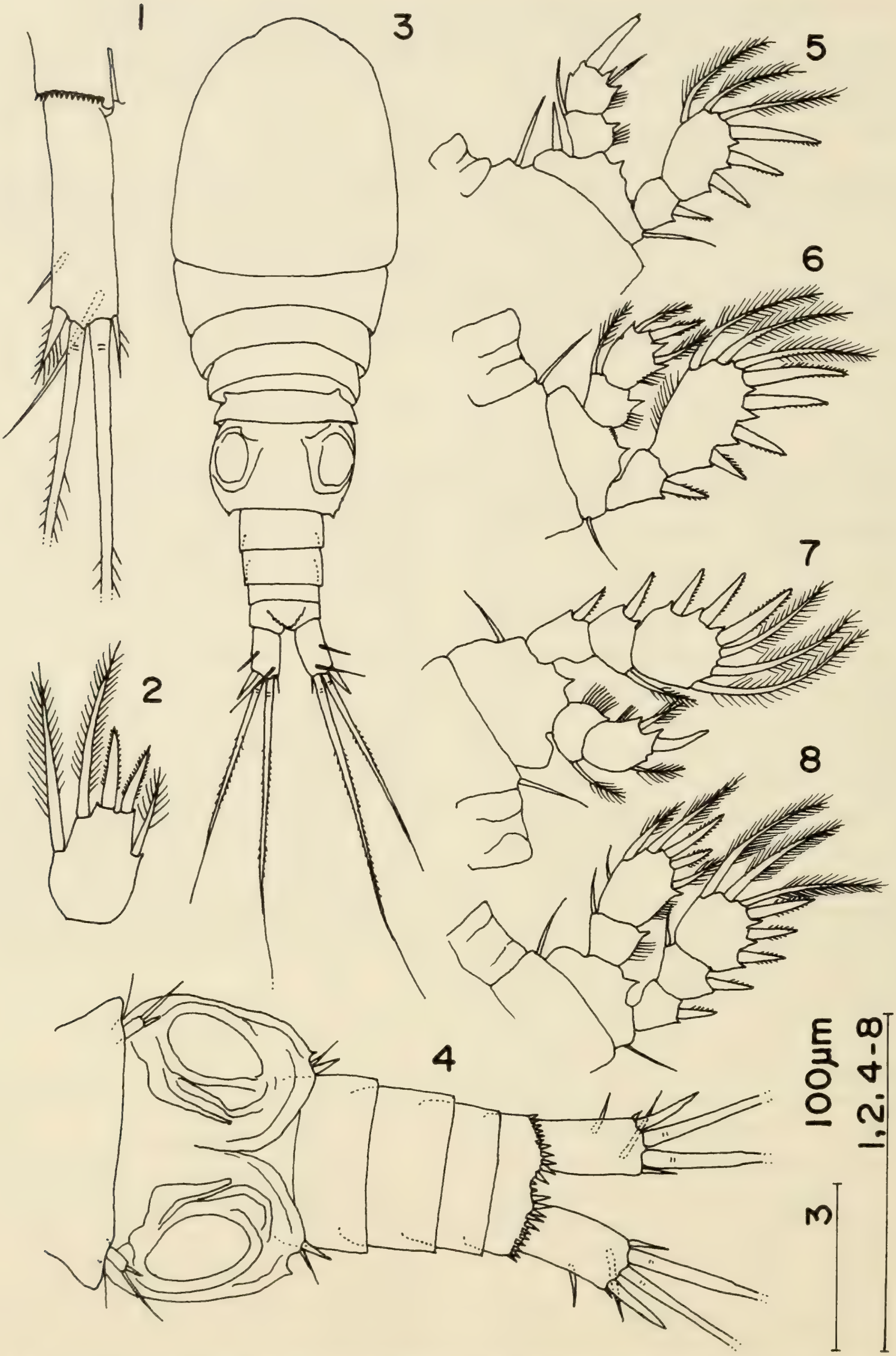
Remarks.—The caudal rami are slender (Fig. 1). 4 times as long as wide, similar to the typical form of the species (Rylov 1948). The distal segment of the endopodite of leg 4 is 1.35 times as long as wide (Fig. 2); the value of this ratio is less than the typical form, but larger than var. *disjunctus* Thallwitz, 1927.

In North America, this species is known from Quebec (Leblanc et al. 1981), and southeastern New York (Strayer 1988 [1989]). Four unpublished collections of this species were made from pitcher plants (*Sarracenia purpurea*) at Belchertown Bog, near Amherst, Massachusetts in 1972 by Dr. D. Fish, University of Notre Dame, Indiana (a reviewer's communication). This is the first record from western North America.

Speocyclops yezoensis Ito, 1954
Figs. 3–8

Material examined.—1 ♂, dissected on 1 slide: USNM 251163.

Remarks.—Flattened body, triangular anal operculum, short caudal rami, and leg 5 composed of two segments are the characteristics of this species (Ito 1954). Compared to the spine formula of the type, 3,4,3,3 and seta-formula 4,3,4,3, this Alaskan specimen has 3,4,3,3 for spine- and 3,3,3,3 for seta-formula (Figs. 5–8). However, these seta-formulas are included in the range of variation in the Japanese individuals in my collection. The Japanese individuals in my collection have 1 or 2, 2 or



Figs. 1–8. *Diacyclops languidus,* female: 1, caudal ramus, ventral; 2, leg 4 endopodite segment 3. *Speocyclops yezoensis,* male: 3, habitus, dorsal; 4, prosomite 5 and abdomen, ventral; 5, leg 1 and coupler; 6, leg 2 and coupler; 7, leg 3 and coupler; 8, leg 4 and coupler.

3, 4, 3 inner lateral setae of the distal segments of endopodites of legs 1–4, while the Alaskan specimen has 0,1,1,3 (Figs. 5–8). As Figs. 5–7 show, the inner borders of endopodites of legs 1–3 have impressions of lost or degenerated setae.

This species is common in the mountain and subterranean waters of Japan, from Hokkaido to Kyushu. The occurrence in Alaska is the first record from the Nearctic.

Gulcamptus uenoi Miura, 1969
Figs. 9–14

Material examined.—2 ♀♀, dissected on 2 slides, and 3 ♀♀, habitus, on 1 slide: USNM 251164.

Remarks.—Genus *Gulcamptus* is related to genus *Moraria,* but is distinguishable from that by proximal segments of endopodites of legs 2–4 without inner seta. The terminal segment of leg 4 endopodite of females from the type population is armed with 2 setae, and the basipodite of leg 5 with 2 spines, while the corresponding legs of Alaskan specimens bear 2 or 3 setae and 3 spines, respectively (Figs. 13, 14). The anal operculum of the type is armed with a stout protuberance on each corner, but with 4 denticles in Alaskan specimens (Fig. 9). There seem to be no other differences.

This species was described from only 2 females and 4 males collected from a cave in South Korea (Miura 1969). No subsequent records exist.

The absence of records from Japan, where it has been collected intensively, and the occurrence in North America are interesting from the viewpoint of biogeography.

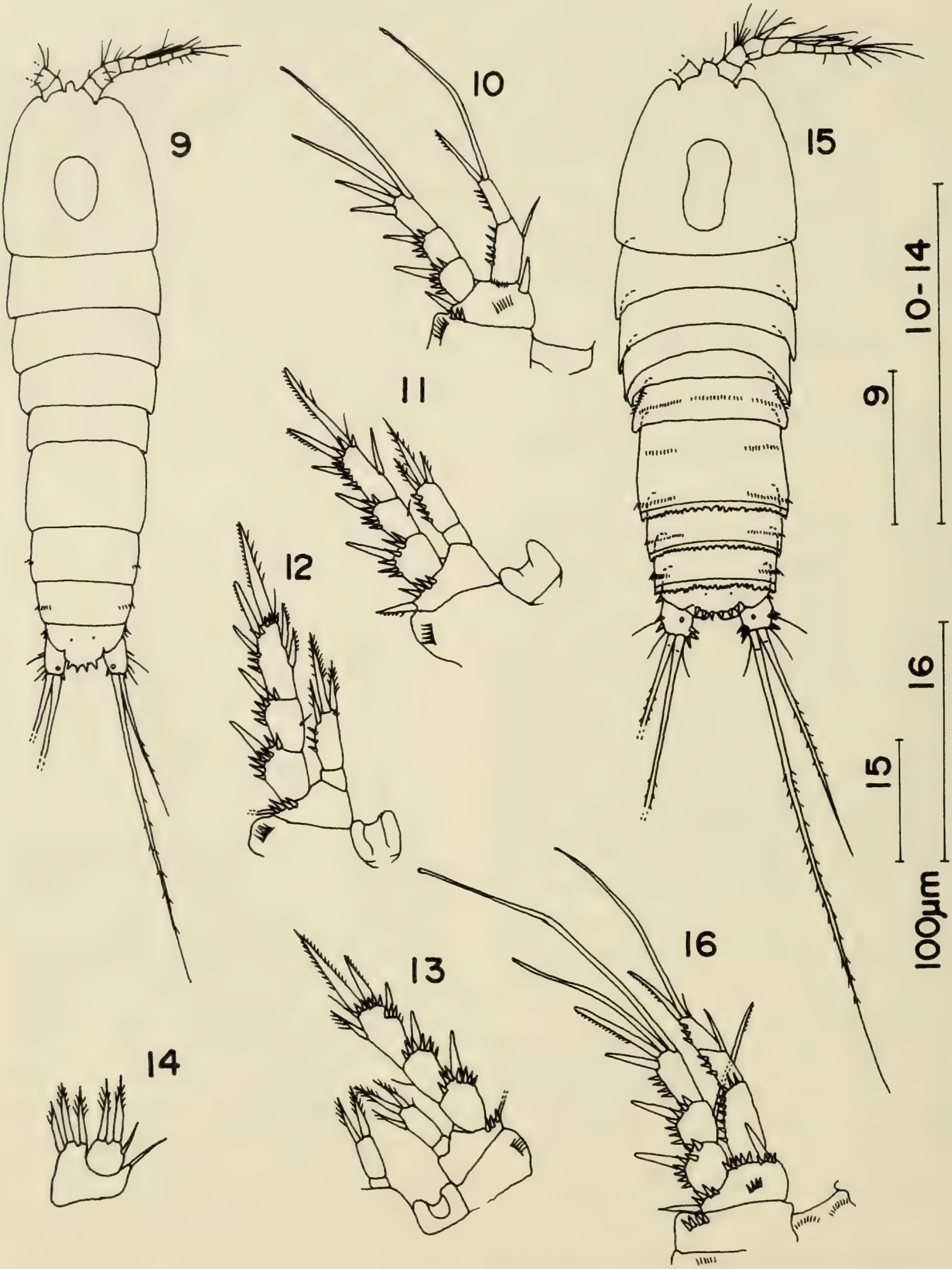
Bryocamptus hiatus (Willey, 1925)
Figs. 15–26

Material examined.—14 ♀♀, dissected on 8 slides, and 2 ♂♂ dissected on 2 slides; 2 ♀♀, and 2 ♂♂, habitus, on 2 slides: USNM 251165.

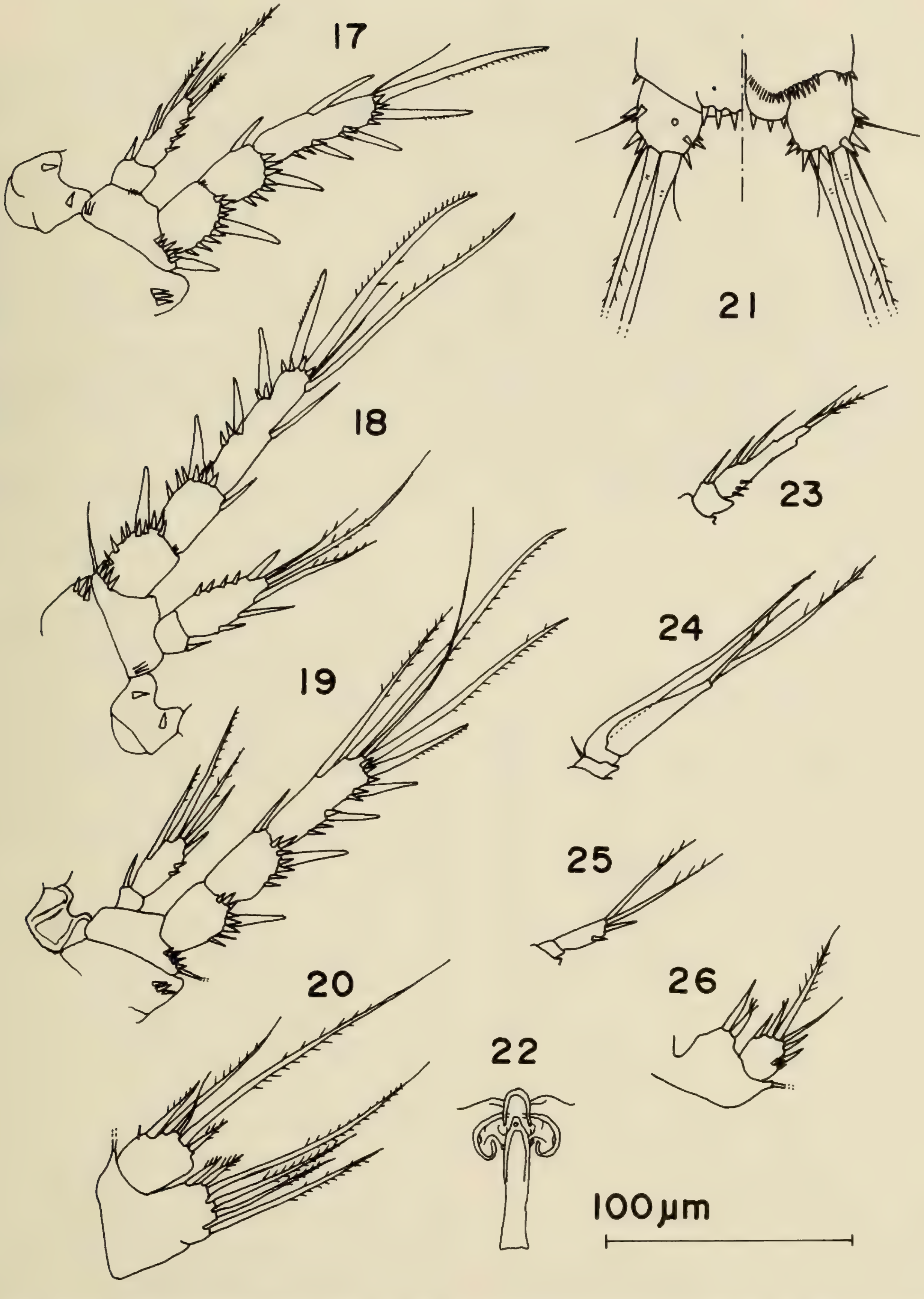
Remarks.—This species is closely related to *Bryocamptus zschokkei* (Schmeil, 1893), but is discriminated from the latter by leg 1 endopodite composed of three segments, and female caudal rami with spinules around the medioposterior corner. On legs 2–5 (Figs. 17–20, 23–26), the spine- and seta-formula of the Alaskan specimens of this species are the same as those of *B. zschokkei,* except the terminal segment of leg 4 endopodite of the male. At this location, *B. zschokkei* has 1 seta on the medial border, while the Alaskan *B. hiatus* has no seta (Fig. 25). Formulas for major armament of the Alaskan specimens and eastern North American specimens (shown in parentheses), after Willey (1934) and Coker (1934), are as follows:

Female		
	leg 2	exp 1-0; 1-1; 3,2,1
		enp 0-1(0); 1,2,2(1 or 2)
	leg 3	exp 1-0; 1-1; 3,2,2
		enp 0-1; 1,2,3(1 or 2)
	leg 4	exp 1-0; 1-1; 3,2,2
		enp 0-1; 1,2,2(1)
	leg 5	basipodite 6(5)
Male		
	leg 2	enp 0-1; 0,2,2
	leg 4	enp 0-0; 1,2,0(1)

The most conspicuous difference between the Alaskan and eastern North American specimens is the number of setae on the leg 5 basipodite. Alaskan specimens are armed with 2 short setae on the lateral apical corner of the basal expansion (Fig. 20), while eastern specimens bear only 1 seta. In addition to the differences in the formula, the Alaskan specimens' medial apical setae of exopodite segments 2 and 3 of legs 2–4 are considerably shorter than those of eastern specimens. Such deviation between the populations of western and eastern North America may be owing to a geographical barrier such as the Rocky Mountains. At present, however, we have no information on the intermediate populations between southeastern Alaska and eastern North America, and those of the southern and



Figs. 9–16. *Gulcamptus uenoi,* female: 9, habitus, dorsal; 10, leg 1 and coupler; 11, leg 2 and coupler; 12, leg 3 and coupler; 13, leg 4 and coupler; 14, leg 5. *Bryocamptus hiatus,* female: 15, habitus, dorsal; 16, leg 1 and coupler.



Figs. 17–26. *Bryocamptus hiatus,* female: 17, leg 2 and coupler; 18, leg 3 and coupler; 19, leg 4 and coupler; 20, leg 5; 21, caudal ramus, dorsal and ventral; 22, seminal receptacle; male: 23, leg 2 endopodite; 24, leg 3 endopodite; 25, leg 4 endopodite; 26, leg 5.

northern areas. If there is a border of clear discontinuity in the above mentioned discrepancies between the populations, the Alaskan population should be treated as a variety or subspecies of the species.

Discussion

Only a small amount of detritus in a polyethylene bag from Alaska revealed the existence of several cyclopoid and harpacticoid species common to the Palaearctic and Nearctic and western and eastern North America. Further, the specimens revealed morphological variation or deviation between populations separated by long distances and/or geographical barriers, viz. seas or mountains. The variation or deviation in geographically separate populations indicates the necessity of reexamination of species level taxonomy of freshwater copepods over wide ranges.

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TORTANUS (*ACUTANUS*) *ANGULARIS*, NEW SUBGENUS AND NEW SPECIES (COPEPODA: CALANOIDA), FROM THE CARIBBEAN SEA, WITH REMARKS ON THE SUBGENERA IN THE GENUS *TORTANUS*

Susumu Ohtsuka

Abstract.—*Tortanus* (*Acutanus*) *angularis,* new subgenus and new species (Copepoda: Calanoida), is described from Belize. The new subgenus *Acutanus* which accommodates three northwestern Atlantic species, *T. angularis,* n. sp., *T. setacaudatus* Williams, 1906 and *T. compernis* González & Bowman, 1965, is defined and compared with the other subgenera, *Tortanus* Giesbrecht, 1898 and *Atortus,* new subgenus. Diagnoses for these three subgenera are presented with remarks on species distributions. The type species of the genus *Tortanus* Giesbrecht, 1898 and its nominotypical subgenus is newly designated.

During taxonomical and phylogenetic studies on the pelagic calanoid copepod *Tortanus* by the author (Ohtsuka et al. 1987, Ohtsuka & Kimoto 1989), a new species of the genus was found in a plankton sample from the Caribbean Sea, which Dr. F. D. Ferrari (Smithsonian Institution) collected and kindly sent me. This new species is the fourth species from the Atlantic Ocean, and shares morphological characters with two previously known species from the northwestern Atlantic, *T. setacaudatus* Williams, 1906 and *T. compernis* González & Bowman, 1965. All three species cannot be assigned to the subgenera *Tortanus, Eutortanus* and *Atortus* from the Indo-Pacific region, hence a new subgenus is established to accommodate these three species.

A type species has never been fixed for the genus *Tortanus* Giesbrecht, 1898 and its nominotypical subgenus. Moreover, Sewell (1932) established the Indo-West Pacific subgenus *Atortus* without the fixation of a type species. Therefore the subgenus name *Atortus* is not available based on Art. 13(b) of the International Code of Zoological Nomenclature and must be published here as a new subgenus along with the designation of a type species. In the present paper, the type species of these two subgenera are newly designated, and the two new and the nominotypical subgenera are defined in detail.

Materials and Methods

Specimens of the new species of *Tortanus* were included in a plankton sample collected from shallow-water channels (100 cm in depth) of a mangrove cay (Twin Cays) off Belize (16°50′N, 88°05′W, 21 Oct 1985) with a plankton net (mesh size: 110 μm) by Dr. F. D. Ferrari. The new species was compared with *T. setacaudatus* collected from Waquoit Bay, Falmouth, Massachusetts (25 Sep 1925; Dr. C. B. Wilson leg.) and *T. compernis* from Bahía Fosforescente, Puerto Rico (19 Jul 1957; Dr. R. E. Coker leg.), specimens of which I received from Dr. T. E. Bowman in exchange for specimens of other species of *Tortanus.*

All types of the new species are deposited in the National Museum of Natural History, Smithsonian Institution.

Tortanus (*Acutanus*), new subgenus

Diagnosis.—Body slender. Prosome of female about twice as long as urosome. Pedigers 4 and 5 separate; pediger 5 symmetrical. Urosome of female 3-segmented; genital somite nearly symmetrical; genital operculum crescent-shaped; anal somite with acute dorsal process medially, and incompletely fused with caudal rami; 2nd-to-innermost caudal setae of both rami normally thickened and not so swollen as in subgenus *Atortus,* new subgenus (diagnosis of the new subgenus given below). Urosome of male 5-segmented; right posterior margin of 2nd somite produced into spine-like process posteriorly; anal somite separated from caudal rami and having acute dorsal process as in female. Fused segments 19–21 of right antennule of male not so produced terminally as in *Atortus.* Maxillule with 11 setae on arthrite. Basipod 1 of maxilliped bearing 2 large spinulose setae. Legs 1–4 with 2-segmented endopod and 3-segmented exopod; terminal exopod segment of leg 1 with 1 outer spine; terminal exopod segment of leg 2 with 2 outer lateral spines; terminal endopod segments of legs 1–4 each having 6 setae. Leg 5 of female uniramous, 3-segmented; terminal segment bearing 1 outer lateral and 3 terminal spines, innermost of which may be fused to terminal segment. Proximal exopod segment of right leg 5 of male swollen; distal exopod segment originating from near inner base of proximal exopod segment; inner lateral margin of proximal segment facing outer lateral margin of distal exopod segment to form chela.

Type species.—*Tortanus angularis,* new species, by original designation, described below.

Etymology.—The subgeneric name "*Acutanus*" is derived from the Latin acutus, meaning acute and anus, meaning anus, and refers to the acute dorsal process on the anal somites of both sexes.

Remarks.—The new subgenus comprises only three species, *T. angularis,* n. sp., *T. setacaudatus* and *T. compernis. T. angularis* is selected as type species since the oldest species, *T. setacaudatus,* was not fully illustrated in the original description by Williams (1906).

Tortanus (*Acutanus*) *angularis,*
new species
Figs. 1–4, 6

Material examined.—29 ♀♀ (body length 1.04 (mean) ± 0.03 mm (standard deviation), range 0.98–1.09 mm); 80 ♂♂ (body length 0.83 ± 0.02 mm, range 0.77–0.88 mm).

Types.—Holotype: ♀, dissected and mounted on glass slides, USNM 251273. Allotype: ♂, dissected and mounted on glass slides, USNM 251274. Paratypes: 2 ♀♀ & 3 ♂♂, dissected and mounted on glass slides, 20 ♀♀ & 20 ♂♂, whole specimens, USNM 251275.

Description.—*Female* (holotype). Body (Fig. 1A, B) slender, 1.01 mm in length. Eye large, tinged with red. Cephalosome, dorsal side of cephalosome with middle transverse groove and protrusion on middle posterior end; both lateral sides fringed with minute prominences. Pediger 5, both posterior corners symmetrical, rounded. Urosome relatively slender, 3-segmented; genital somite (Fig. 1C) about 1.4 times as long as wide, having crescent-shaped genital operculum; anal somite (Fig. 1D) with strong acute process posterodorsally, fused dorsally with caudal rami; caudal rami (Fig. 1D) slender, nearly symmetrical, bearing minute sensillum in middle of outer margin, with 1 subterminal outer, 1 dorsal and 4 terminal plumose setae; posterior half of inner margin of caudal ramus fringed with hairs. Antennule (Fig. 1E) reaching middle of caudal ramus, consisting of 17 free segments, since segments 1–7, 9–12 and 24–25 are fused (segmentation based on Giesbrecht (1892)); armament on segments 13–23 similar to that of *Tortanus scaphus* (see Table 1, Bowman 1971) except for segments 17 and 19; seg-

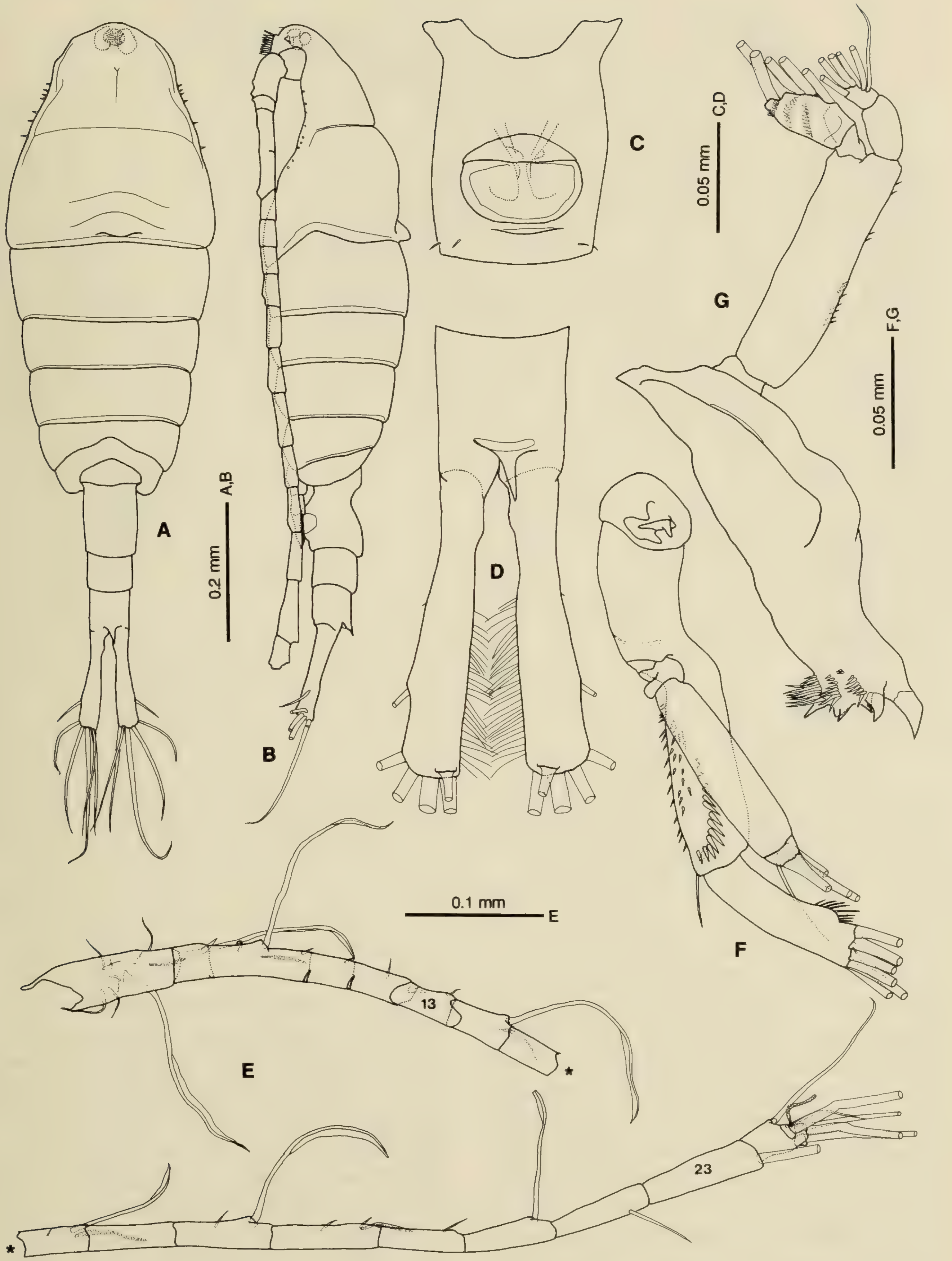

Fig. 1. *Tortanus* (*Acutanus*) *angularis*, new subgenus, new species, female (holotype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Genital somite, ventral view; D, Anal somite and caudal rami, dorsal view; E, Right antennule; F, Antenna; G, Mandible.

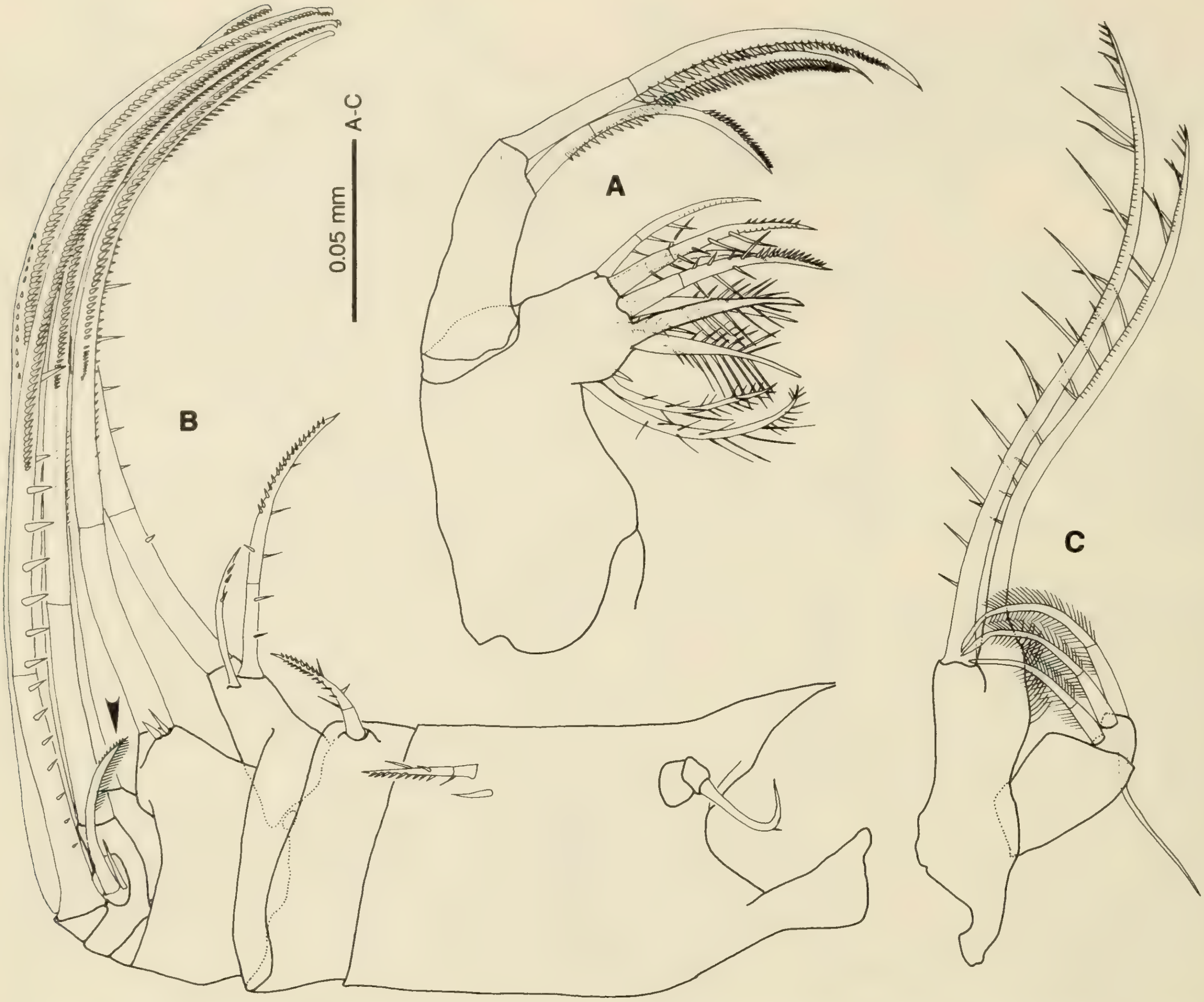

Fig. 2. *Tortanus (Acutanus) angularis,* new subgenus, new species, female (holotype). A, Maxillule; B, Maxilla, arrowhead meaning a relatively developed seta, compared with that of *Tortanus (Atortus) erabuensis* Ohtsuka, Fukuura & Go, 1987; C, Maxilliped.

ment 17 of right antennule unarmed while that of left with 1 aesthetasc; segment 19 with 2 setae and 1 aesthetasc. Antenna (Fig. 1F), basipod 2 fused with endopod, bearing subterminal seta; endopod 2-segmented, proximal segment bearing subterminal seta, row of spinules, and patch of minute spinules on outer surface, apical segment with 6 terminal setae and small inner knob with tuft of spinules; exopod 3-segmented, proximal segment unarmed, middle segment with 1 subterminal and 2 terminal setae, and distal segment bearing 2 apical setae. Mandible (Fig. 1G), mandibular cutting edge with 5 cusped teeth; 2 ventral teeth monocuspid with crown; basipod elongate, sparsely fringed with minute spinules on inner margin; endopod 2-segmented, proximal segment unarmed, apical segment with 6 setae of unequal lengths; exopod with 5 setae and 3 rows of minute spinules on surface. Maxillule (Fig. 2A), arthrite developed, bearing 10 setae and 1 small seta; 2nd inner lobe elongate, bearing 3 thick, serrate setae. Maxilla (Fig. 2B) similar to that of *T. erabuensis* (see Fig. 2B, Ohtsuka et al. 1987), but differing in the following points: no spinules along inner margin; 3rd inner lobe without fine setule; inner small serrate seta (indicated by an arrowhead in Fig. 2B) relatively well-developed; inner terminal seta with large spinules along inner basal

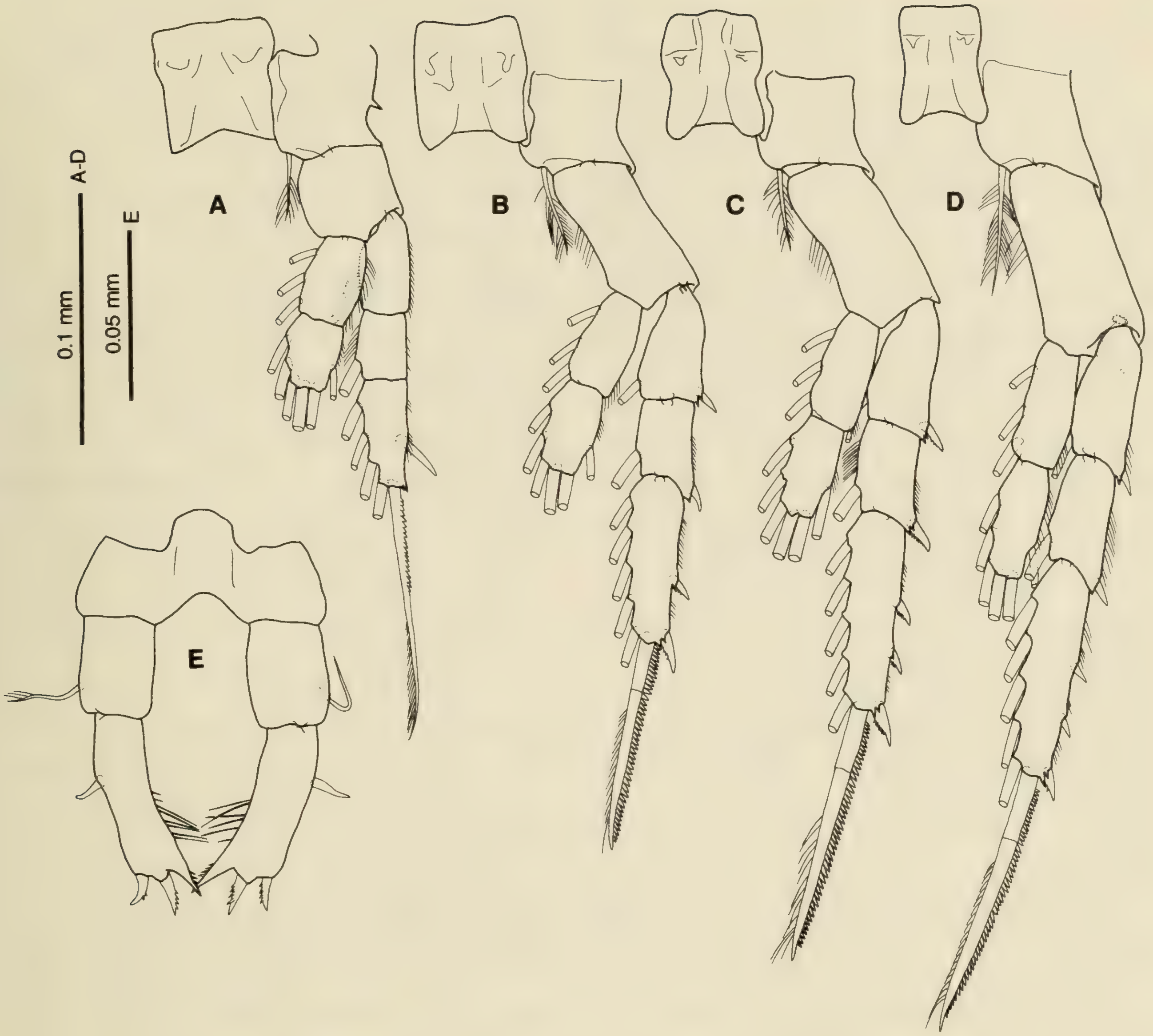

Fig. 3. *Tortanus* (*Acutanus*) *angularis,* new subgenus, new species, female (holotype). A, Leg 1, anterior surface; B, Leg 2, anterior surface; C, Leg 3, anterior surface; D, Leg 4, anterior surface; E, Leg 5, anterior surface.

margin. Maxilliped (Fig. 2C), basipod 1 produced anteriorly, and bearing 2 spinulose setae terminally; basipod 2 unarmed; endopod with 3 thick, plumose inner setae and 1 seta directed posteriorly. Legs 1–4 each with 2-segmented endopod and 3-segmented exopod. Leg 1 (Fig. 3A), basipod 1 with inner distal plumose seta and acute outer prominence; terminal exopod segment bearing middle outer spine and terminal seta serrate along proximal part of outer margin. Leg 2 (Fig. 3B), terminal exopod segment with 2 outer serrate spines. Leg 3 (Fig. 3C), terminal exopod segment bearing 3 outer spines. Leg 4 (Fig. 3D), basipod 2 with seta on posterior surface; terminal exopod segment having 3 outer spines. Leg 5 (Fig. 3E) nearly symmetrical; 1st basipods completely fused with intercoxal plate to form common base; basipod 2 with fine seta at a point of about two-thirds outer margin; exopod 1-segmented, longer than basipod 2; exopod bearing 3 serrate terminal spines, innermost fused with segment; outer spine at a point of one-third margin from base; relatively long spinules along distal half of inner margin.

Male (allotype: Figs. 4A–E, 6A; paratype:

Fig. 4F).—Body (Fig. 4A, B) slenderer than in female, 0.85 mm in length. Urosome 5-segmented; genital somite slightly more produced on left lateral side at genital opening than on right side; 2nd urosomal somite remarkably protruded posteriorly at right posterior corner into acute process, which reaches to one-third length of 3rd somite and bears subterminal and basal setules (Fig. 4C); anal somite with acute mid-dorsal process, articulating with caudal rami; right caudal ramus slightly shorter than left caudal ramus, and right caudal ramus only with tuft of hairs along proximal half outer margin. Right antennule (Fig. 4D) geniculate; segments 1–5 (a seta missing in Fig. 4D), 7, 14, and 16 having long seta with distal flange; segments 7–12 incompletely fused (the number for each segment is based on Giesbrecht (1892)); segments 9 and 12 each with thick, short seta anteriorly; segment 17 with serrate flange along anterior margin slightly produced distally, and subterminal seta; segment 18 also with serrate anterior flange and subterminal seta; fused segments 19–21 with 2 serrate ridges anteriorly, proximal ridge short and distal ridge two-thirds length of segment, and terminal seta (Fig. 6A). Leg 5 (Fig. 4E, F), right leg: 1st and 2nd basipods fused, swollen; proximal exopod segment expanded, with plumose seta near the base on anterior surface and 2 fine setae distally; apical exopod segment spatulate, bearing 2 minute setae along concave outer margin and terminal setule, and its outer distal tip corrugate. Left leg: basipod 1 unarmed; basipod 2 elongate, bearing seta at a point of two-thirds of outer margin and inner seta at midlength; proximal exopod segment with subterminal outer and middle inner setae; distal exopod segment having 2 inner and 2 outer setae and relatively long terminal seta.

Etymology.—The specific name "*angularis*" refers to the acute ventrolateral process on the right posterior margin of the second urosomal somite of the male.

Comparison.—Females of the new species are smaller than those of *T. setacaudatus* (1.25–1.4 mm, Wilson 1932) and *T. compernis* (1.14.–1.19 mm, González & Bowman 1965); males of the new species are also smaller than those of *T. compernis* (1.02–1.08 mm, González & Bowman 1965) but are within the body length range of *T. setacaudatus* (0.75–0.95 mm, Wilson 1932).

Anal somites, caudal rami and legs 5 of females, and urosomes and legs 5 of males of *T. setacaudatus* and *T. compernis* are illustrated in Fig. 5. The dorsal process on the female anal somite is relatively longer in *T. angularis* (Fig. 1D) than in the other two species (Fig. 5A, B). The caudal ramus of female of *T. angularis* is slenderer than that of *T. setacaudatus*; its inner margin is not as straight as in the latter and is constricted at a point of about one-fourth along its length. In *T. compernis* (see Fig. 5B), both caudal rami are "in contact or nearly so near the base" (González & Bowman 1965), and have a ventral tuft of long hairs anteriorly. The terminal segment of leg 5 of female *T. angularis* is similar to that of *T. compernis* in that the innermost terminal spine is fused with the segment to form a process, but differs from that of *T. compernis* by the relative position of terminal spines: the innermost spine is not as widely separated from the remaining two spines in *T. angularis* as in *T. compernis* (Figs. 3E, 5D). The innermost spine of *T. setacaudatus* is articulated with the segment (Fig. 5C).

In the male, the posterolateral process on the right side of the second urosomal somite is species-specific. In *T. angularis,* the process is strongly produced posteriorly to reach one-third the length of the third urosomal somite (Fig. 4A, B). In *T. setacaudatus* (Fig. 5E, F), the process is relatively small and produced outward, while in *T. compernis* (Fig. 5G–I) the process is irregularly produced outward and more developed than in *T. setacaudatus.* A tuft of hairs on the right lateral side of the anal somite is present only in *T. compernis.* The location of a tuft of hairs on the right caudal ramus of the male is different among these three species. In *T.*

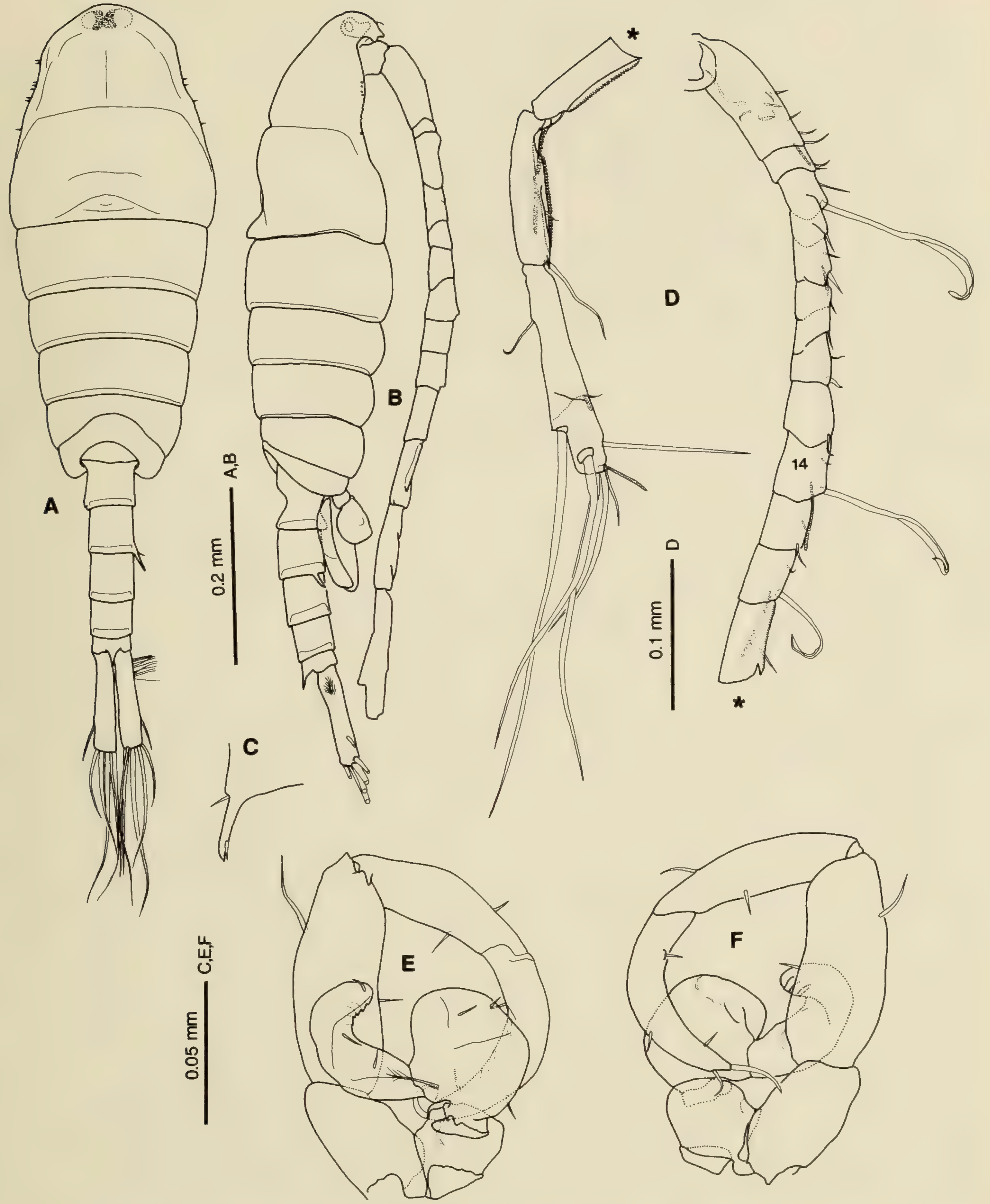

Fig. 4. *Tortanus* (*Acutanus*) *angularis,* new subgenus, new species, male (allotype: A–E; paratype: F). A, Habitus, dorsal view; B, Habitus, lateral view; C, Posterolateral process of second urosomal somite, ventral view; D, Right antennule; E, Leg 5, anterior surface; F, Leg 5, posterior surface.

angularis and *T. setacaudatus,* the tuft is found within the anterior half, whereas in *T. compernis* it is present along the posterior half of the outer margin. Legs 5 of males of *T. setacaudatus* and *T. compernis* are shown in Fig. 5J and K, respectively. A subterminal outer seta of basipod 1 of left leg 5 is relatively longer in *T. angularis* (Fig. 4E, F)

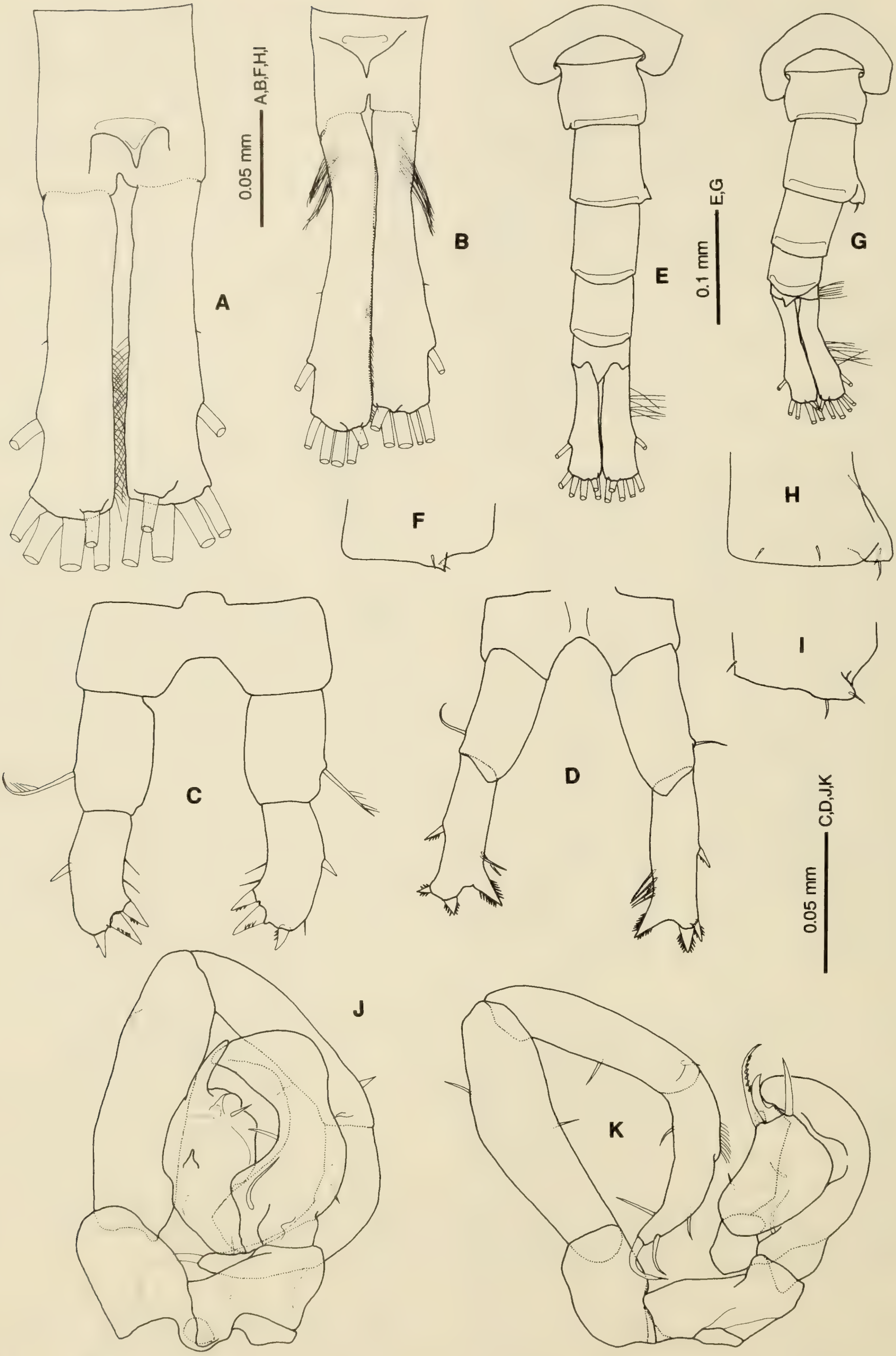

Fig. 5. *Tortanus* (*Acutanus*) *setacaudatus* Williams, 1906 (A, C, E, F, J) and *Tortanus* (*Acutanus*) *compernis* González & Bowman, 1965 (B, D, G–I, K). A, B, Anal somites and caudal rami of females, dorsal view; C, Leg

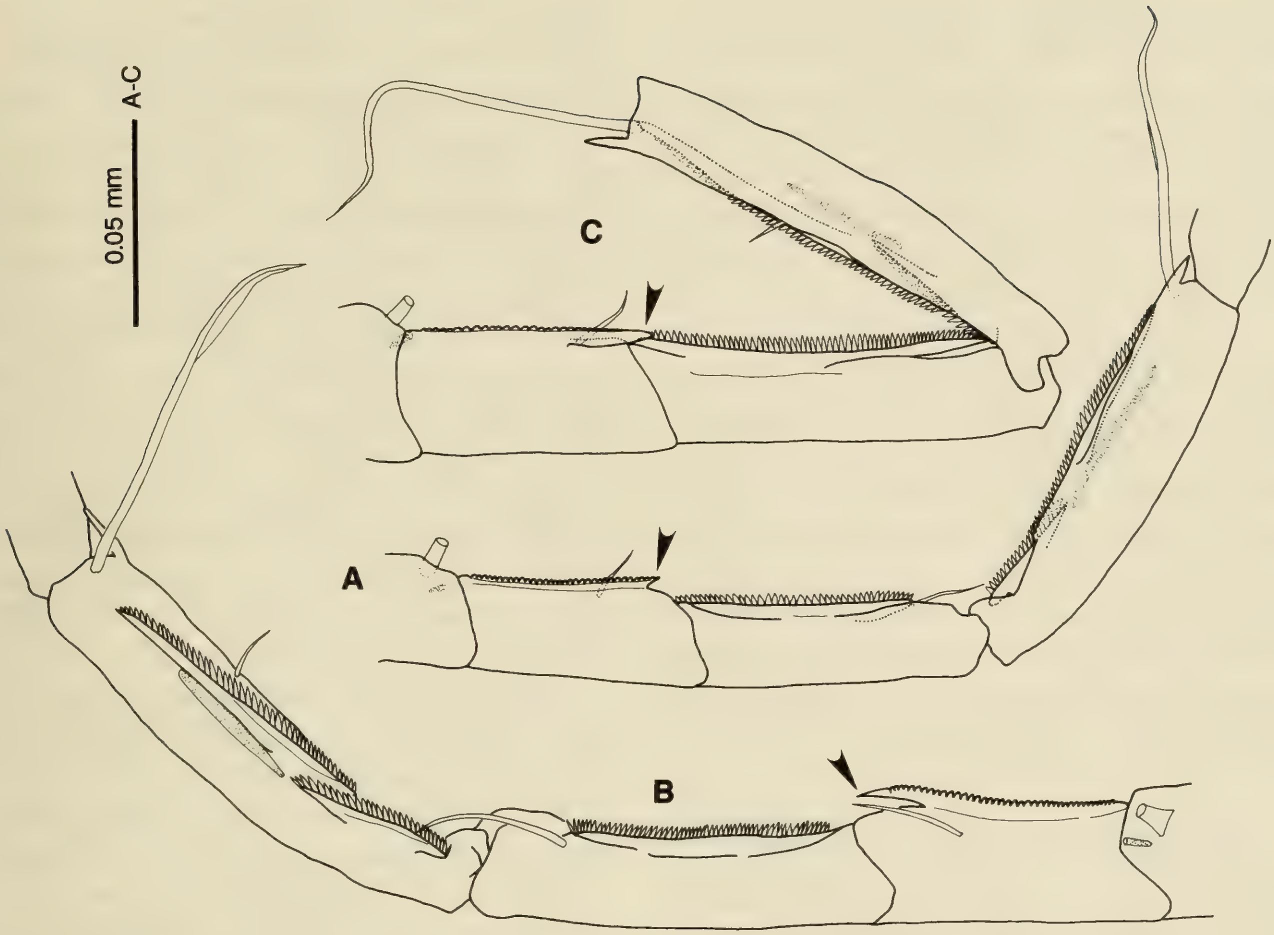

Fig. 6. Grasping portions of male right antennules of *Tortanus* (*Acutanus*) *angularis,* new subgenus, new species (allotype) (A), *Tortanus* (*Acutanus*) *setacaudatus* Williams, 1906 (B), and *Tortanus* (*Acutanus*) *compernis* González & Bowman, 1965 (C). An arrowhead means an anterodistal process of segment 17.

than in *T. setacaudatus* and *T. compernis.* Right legs are remarkably different among the three species. Structures of chelae of the latter two species are similar in having a concave inner margin of the proximal exopod segment while the bulb-like proximal exopod segment of *T. angularis* is unique.

Grasping portions of male right antennules of *T. angularis, T. setacaudatus* and *T. compernis* are depicted in Fig. 6. An anterodistal process of segment 17 (indicated by arrowheads in Fig. 6) is long enough to reach the distal end of the segment in *T. setacaudatus* (Fig. 6B) and *T. compernis* (Fig. 6C), while that of *T. angularis* is short (Fig. 6A).

Remarks on the Subgenera of *Tortanus*

The genus *Tortanus* presently comprises four nominal subgenera, *Tortanus, Atortus, Eutortanus,* and *Acutanus* (Sewell 1932, Smirnov 1935, present study). Smirnov (1935) assigned *T. derjugini* Smirnov, 1935, *T. discaudatus* (Thompson & Scott, 1897) and *T. setacaudatus* to the less known subgenus *Eutortanus* whose name was suggested first in a communication to Smirnov by Steuer (see Smirnov 1935). According to Art. 8(a) of the International Code of Zoological Nomenclature, Smirnov (1935) is responsible for the subgeneric name. *Eutortanus* corresponds to the first of Steuer's (1926)

←

5, anterior surface; D, Leg 5, posterior surface; E, G, Urosomes of males, dorsal view; F, I, Posterolateral processes of second urosomal somites, lateral view; H, Posterolateral process of second urosomal somite, dorsal view; J, K, Legs 5, anterior surface.

groups of species or *setacaudatus–discaudatus*-group (Smirnov 1935). However, this group is not a monophyletic lineage as discussed below. Since *T. derjugini* should be alone in the subgenus *Eutortanus,* the type species is fixed by monotypy (the International Code of Zoological Nomenclature, Art. 13(c)). Presently the subgenus *Eutortanus* accommodates five northeastern Asian species (*T. derjugini, T. dextrilobatus* Chen & Zhang, 1965, *T. sheni* Hulsemann, 1988, (=*T. denticulatus* Shen & Lee, 1963), *T. spinicaudatus* Shen & Bai, 1956, *T. vermiculus* Shen, 1955) (present study). A new subgenus should be erected for the remaining North Pacific species incorporating the North Atlantic, *T. discaudatus. Eutortanus* and the new subgenus will be discussed in detail in a forthcoming paper.

Tortanus (*Acutanus*), new subgenus

Remarks.—Considering the morphological and zoogeographical relationships between species of the genus *Tortanus,* Steuer (1926) proposed three distinct groups within the genus, (1) *setacaudatus-discaudatus*-group, (2) *gracilis-forcipatus-barbatus*-group, and (3) *murrayi-brevipes-recticauda*-group. Later, Sewell (1932) regarded the latter two groups classified by Steuer (1926) as two subgenera, namely, *Tortanus* and *Atortus* (see Bowman 1971). Although *T. discaudatus* and *T. setacaudatus* have parapatric distributions in the northwestern Atlantic Ocean (e.g., Steuer 1926, Wilson 1932, Brodsky 1950), Steuer's (1926) *setacaudatus–discaudatus*-group is incorrect, because of the following morphological differences between these two species: the number of endopod segments of leg 1 is 2 in *T. setacaudatus,* but 3 in *T. discaudatus*; pedigers 4 and 5 are separate in *T. setacaudatus,* but fused in *T. discaudatus* (Wilson 1932, Mori 1937). By contrast, *T. discaudatus* is more closely related to the five northeastern Asian species mentioned above (*T. derjugini, T. dextrilobatus, T. sheni, T. spinicaudatus, T. vermiculus*) in sharing the following characters, (1) fused pedigers 4 and 5, (2) 5 setae on basipod 2 of maxilliped, (3) 3-segmented endopod of leg 1, (4) 2 outer lateral spines of the terminal exopod segment of leg 1, and (5) 5th legs of both sexes of similar construction. The intrusion of *T. discaudatus* from the North Pacific into the northwestern Atlantic Ocean might have originated from migration during the latest post-glacial or interglacial period in the Pleistocene (cf. Ekman 1953, Nishimura 1981), which resulted in the present-day contiguous but secondary distributions of *T. discaudatus* and *T. setacaudatus.* However, *T. setacaudatus* comprises a monophyletic lineage with *T. angularis* and *T. compernis.*

Distribution.—The subgenus is exclusively distributed in the northwestern Atlantic region. *T. setacaudatus* has the widest distribution from Woods Hole in the north to the northern part of the Gulf of Mexico (González & Bowman 1965). *T. compernis* was recorded only in the type locality, Bahía Fosforescente, Puerto Rico. *T. angularis* is reported only from off Belize (present study).

According to Fleminger (1957), the northern neritic region of the Gulf of Mexico is characterized by a warm temperate water indicator, *Labidocera aestiva* Wheeler, 1901, while the remaining neritic waters of the Gulf are dominated by a subtropical/tropical water indicator, *L. scotti* Giesbrecht, 1897. Hence, supposing a strict allopatry of *T. angularis* and *T. setacaudatus,* a habitat partition of both species appears not unlikely: *T. setacaudatus* is likely to be distributed in the northern warm temperate region of the Gulf, while the subtropical/tropical *T. angularis* may occupy the southern part of the Gulf as its northernmost occurrence.

Tortanus (*Tortanus*) Giesbrecht,
in Giesbrecht & Schmeil, 1898

Type species.—*Corynura gracilis* Brady, 1883, by subsequent designation.

Remarks.—The subgenus consists of three species, *T. gracilis* (Brady, 1883), *T. barbatus* (Brady, 1883) and *T. forcipatus* (Giesbrecht, 1889). Based on Art. 69(a) of the International Code of Zoological Nomenclature, *T. gracilis* is selected as the type species of the genus and its nominotypical subgenus. Although *T. barbatus* is one of the originally included nominal species, the original illustrations of *T. gracilis* are more detailed than those of *T. barbatus* (see Brady 1883) and *T. gracilis* is hereby designated as the type species.

Diagnosis.—According to Steuer (1926) and Sewell (1932), the subgenus is defined as follows: prosome of female approximately 1.5 times as long as urosome; pedigers 4 and 5 separate; urosome elongate, 3-segmented in female; both right and left caudal rami of female fused with anal somite; endopod of leg 1 2-segmented; terminal endopod segments of legs 3 and 4 having 7 and 6 setae, respectively (according to my observation of *T. forcipatus* and *T. gracilis,* Sewell's (1932) statement that the terminal endopod segments of both legs 3 and 4 have 7 setae was not correct). In addition, both sexes of these three species have a terminal dorsal process on each caudal ramus unique to this subgenus (see Chen & Zhang 1965, Greenwood 1978). Moreover, although I have not examined *T. barbatus* yet, both *T. forcipatus* and *T. gracilis* share the following characters: terminal exopodal segments of legs 1 and 2 with 2 and 3 lateral spines, respectively; terminal endopodal segment of leg 2 with 7 setae; maxillulary arthrite with 12 setae; basipod 1 of maxilliped having 5 setae.

Distribution.—The distributions of the three species are partly overlapping in the Indo-West Pacific. However, only *T. barbatus* occurs in South Australian waters, but has hitherto not been reported from Japanese and Chinese waters (Greenwood 1978). *T. forcipatus* and *T. gracilis* have a sympatric distribution in the Indo-West Pacific region (Giesbrecht 1892, Giesbrecht & Schmeil 1898, Scott 1909, Steuer 1926, Mori 1937, Chen & Zhang 1965, Tanaka 1965, Madhupratap & Haridas 1986) but no occurrence of these two species has been reported from the East African coast. In the Red Sea all three species were recorded (Giesbrecht 1892, Giesbrecht & Schmeil 1898, Scott 1909, Steuer 1926, Tanaka 1965, Greenwood 1978).

Tortanus (*Atortus*), new subgenus

Type species.—*Tortanus murrayi* Scott, 1909, by original designation.

Remarks.—Sewell (1932) newly established the subgenus *Atortus* in which four species, *T. recticauda* (Giesbrecht, 1889), *T. brevipes* Scott, 1909, *T. murrayi* Scott, 1909 and *T. tropicus* Sewell, 1932 were included. However, Sewell (1932) did not designate any of them as type species. A genus-group name newly published after 1930 must be accompanied with the fixation of a type species (Art. 13(b) of the International Code of Zoological Nomenclature). Hence the subgenus name *Atortus* dissatisfies the criteria of availability. By the fixation of the type species, a new subgenus *Atortus* whose name is the same as Sewell (1932) proposed before becomes available in the present paper. Since *T. murrayi* is one of the well illustrated species in the subgenus and the lectotype and four paralectotypes Bowman (1971) designated are preserved at the University of Amsterdam, Zoological Museum at present, it is designated as type species. 16 species and one undescribed species which are discussed in Ohtsuka & Kimoto (1989) are assigned to the new subgenus: *T. recticauda, T. brevipes, T. murrayi, T. tropicus, T. longipes* Brodsky, 1950, *T. rubidus* Tanaka, 1965, *T. giesbrechti* Jones & Park, 1968, *T. lophus* Bowman, 1971, *T. scaphus* Bowman, 1971, *T. capensis* Grindley, 1978, *T. sinicus* Chen, 1983, *T. bonjol* Othman, 1987, *T. bowmani* Othman, 1987, *T. erabuensis* Ohtsuka, Fukuura & Go, 1987, *T. digitalis* Ohtsuka & Kimoto, 1989, *T. ryukyuensis* Ohtsuka & Kimoto, 1989, *T.* sp. from South Yemen.

Diagnosis.—By reference to the previous works by Sewell (1932), Bowman (1971), Ohtsuka et al. (1987) and Ohtsuka & Kimoto (1989), the new subgenus is defined as follows. Prosome of female about 3 times as long as urosome; pedigers 4 and 5 fused; urosome of female 2- or 3-segmented; caudal rami not as elongate as in subgenus *Tortanus*; maxillulary arthrite with 13 setae; basipod 1 of maxilliped with 2 long setae; endopod of leg 1 2-segmented; terminal endopod segments of legs 3 and 4 with 6 setae.

An additional study of the morphology of *Atortus* revealed that the following characters combined are also unique to this subgenus: terminal exopod segment of leg 1 and leg 2 bearing 1 and 3 outer spines, respectively; terminal endopod segment of leg 2 with 6 setae.

Distribution.—The distributions of the 17 species within the subgenus were discussed in detail in my previous work (Ohtsuka & Kimoto 1989). All the species are exclusively distributed in the Indo-West Pacific region (Ohtsuka & Kimoto 1989).

Acknowledgments

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EURYTE VERECUNDA, NEW SPECIES (COPEPODA: CYCLOPOIDA), ASSOCIATED WITH THE CORAL *PORITES LOBATA* ON THE PACIFIC COAST OF PANAMA

Arthur G. Humes

Abstract.—A cyclopoid copepod, *Euryte verecunda,* is described from 12 m in the Bay of Panama where it is associated with the scleractinian coral *Porites lobata.* Association of *Euryte* with a coral has been reported previously only in the case of *Euryte bellatula,* a closely related species, with *Montipora* in New Caledonia.

The scleractinian coral *Porites lobata* Dana, 1846, is widespread in the tropical Pacific from the Nicobar Islands east to Panama (Glynn et al. 1972, Veron 1986). Several poecilostomatoid copepods are associated with this coral: *Kombia incrassata* Humes, 1984b, and *Monomolgus torulus* Humes, 1984b, at Moorea, and *Hemicyclops columnaris* Humes, 1984a, in Panama.

A new species of the cyclopoid genus *Euryte* is now reported associated with *Porites* in Panama. Although most species of *Euryte* are free-living, one species, *Euryte bellatula* Humes, 1991, has been found associated with six species of the coral genus *Montipora* in the southwest Pacific.

Order Cyclopoida Burmeister, 1834
Family Cyclopidae Dana, 1853
Genus *Euryte* Philippi, 1843
Euryte verecunda, new species
Figs. 1, 2, 3

Type material.—25 ♀♀, 7 ♂♂ from *Porites lobata* Dana, 1846, in 12 m, north side of Uraba Island, near Taboga Island, Bay of Panama, 08°47′N, 79°32′W, 29 Oct 1981. Holotype ♀ (USNM 257115), allotype, (USNM 257116), and 25 paratypes (20 ♀♀, 5 ♂♂) (USNM 257117) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes in the collection of the author.

Other specimens (all from *Porites lobata* at the type locality in 1991).—30 ♀♀, 1 ♂, 29 Oct; 4 ♀♀, 4 ♂♂, 30 Oct; 28 ♀♀, 1 ♂, 5 Nov; 27 ♀♀, 3 ♂♂, 5 Nov.

Female.—Body (Fig. 1a) moderately slender and elongate. Length (not including setae on caudal rami) 0.77 mm (0.74–0.81 mm) and greatest width 0.26 mm (0.24–0.26 mm), based on 10 specimens in lactic acid. Greatest dorsoventral thickness 0.20 mm. Ratio of length to width of prosome 1.82:1. Ratio of length of prosome to that of urosome 1.28:1.

Segment bearing leg 5 (Fig. 1b) 34 × 94 μm in dorsal view. Genital segment elongate, 99 μm long, 78 μm wide at slight anterior expansions, 56 μm wide posteriorly. Lateral spiniform process on both sides almost midlength of segment (Fig. 1c). Genital areas, both with 2 minute setae, located far forward dorsolaterally at widest part of segment (Fig. 1b), both connected by duct to single midventral copulatory pore (Fig. 1d). Three postgenital segments from anterior to posterior 43 × 52, 31 × 49, and 42 × 45 μm.

Caudal ramus (Fig. 1e, f) elongate, in specimen drawn 81 × 13 μm, ratio 6.23:1 ($n = 56$, average 81.3 × 13.9 μm, ratio 5.85:1). Range of length 73–91 μm, range of width 13–15 μm. Outer lateral seta 15 μm, dorsal

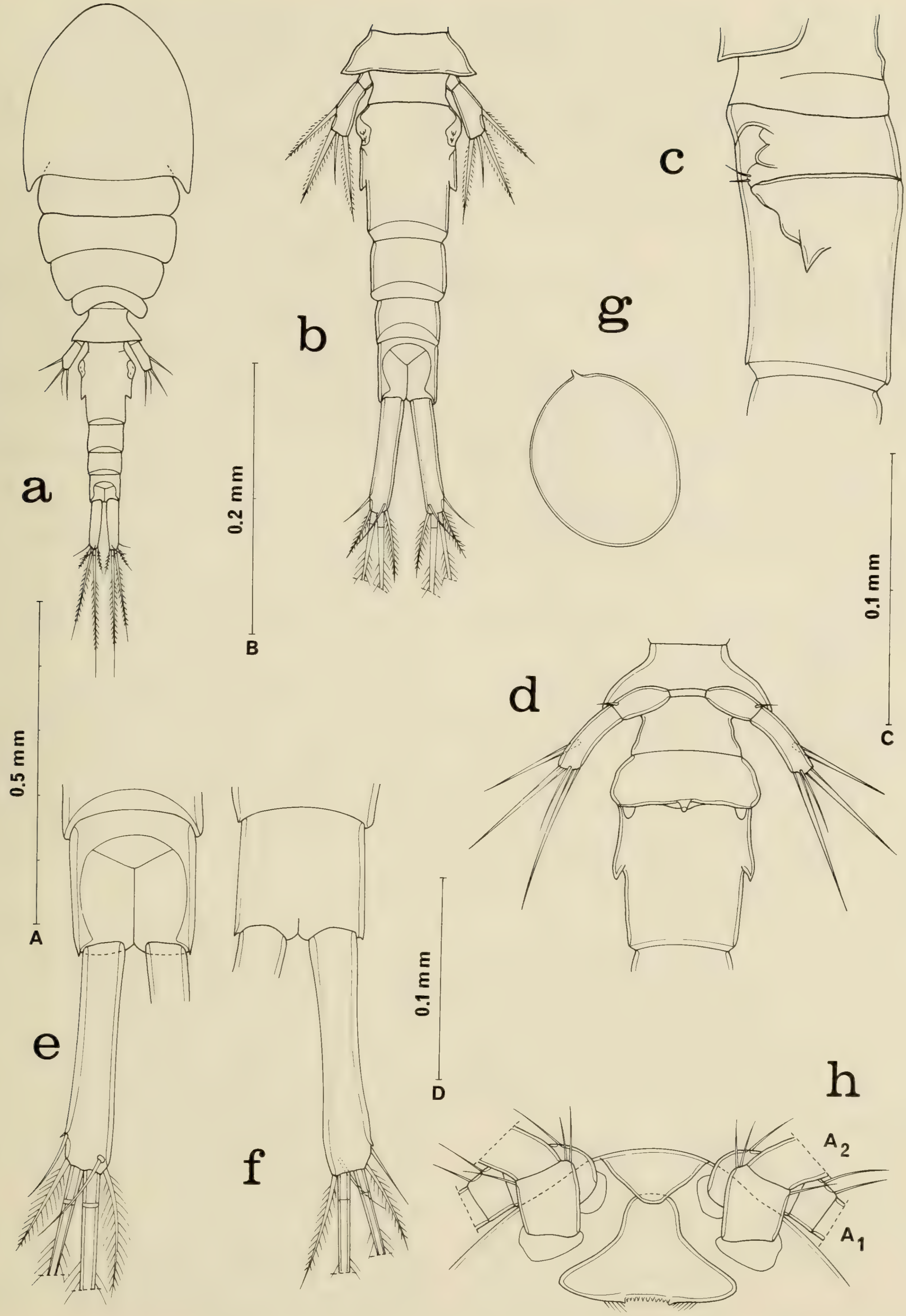

Fig. 1. *Euryte verecunda,* new species, female. a, dorsal view (scale A); b, urosome, dorsal (B); c, genital segment, lateral (C); d, segment bearing leg 5 and genital segment, ventral (C); e, anal segment and caudal ramus, dorsal (C); f, anal segment and caudal ramus, ventral (C); g, egg sac, inner (B); h, rostrum and labrum, ventral (D). A_1 = first antenna, A_2 = second antenna.

seta 44 μm, both smooth. Outermost terminal seta 47 μm, innermost terminal seta 65 μm, and 2 long median terminal setae 180 μm (outer) and 234 μm (inner), all with lateral setules. Frequently caudal ramus slightly constricted as in Fig. 1f, 80 × 13 μm, ratio 6.15:1, width distally 16 μm.

Body surface lacking visible ornamentation.

Egg sac (Fig. 1g) in 22 females containing 1 egg, 128 × 104 μm.

Rostrum (Fig. 1h) broadly linguiform. First antenna (Fig. 2a) 250 μm long, 21-segmented. Lengths of segments (measured along their posterior nonsetiferous margins): 35 (47 μm along anterior margin), 21, 10.5, 8, 8, 8, 8, 8, 9, 10.5, 11, 9, 9, 9, 10.5, 9, 9, 9, 13, 15.5, and 18 μm, respectively. Formula for armature: 8, 3, 2, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 0, 1, 1, 1, 1, 2, 2, and 8. All setae smooth.

Second antenna (Fig. 2b) with 3 of 6 setae on last segment geniculate.

Labrum (Figs. 1h, 2c), mandible (Fig. 2d), first maxilla (Fig. 2e), second maxilla (Fig. 2f), and maxilliped (Fig. 2g) resembling those of *Euryte bellatula.*

Legs 1–4 (Figs. 2h, 3a–c) segmented and armed as in *E. bellatula.* Leg 1 with inner spine on basis 36 μm. Third segment of exopod of leg 4 with terminal spine 55 μm and adjacent outer spine 29 μm.

Leg 5 (Fig. 1d) with first segment 23 × 13 μm in ventral view, its seta 5 μm. Second segment 39 × 10.5 μm, its 4 setae from outer to inner 45, 60, 32, and 68 μm. In flat view, second segment 39 × 17 μm (Fig. 3d).

Leg 6 represented by 2 small setae on genital area (Fig. 1b, c).

Color of living specimens unknown.

Male.—Body (Fig. 3e) with general form resembling that of female. Length 0.62 mm (0.59–0.64 mm) and greatest width 0.19 mm (0.18–0.19 mm), based on 4 specimens in lactic acid. Greatest dorsoventral thickness 0.14 mm. Ratio of length to width of prosome 1.81:1. Ratio of length of prosome to that of urosome 1.32:1.

Segment bearing leg 5 (Fig. 3f) 31 × 68 μm. Genital segment in dorsal view 52 × 60 μm, slightly wider than long with rounded lateral margins. Four postgenital segments from anterior to posterior 34 × 42, 29 × 39, 24 × 36, and 29 × 34 μm.

Caudal ramus similar to that of female but shorter, 62 × 13 μm, ratio 4.77:1.

Body surface smooth as in female.

Rostrum like that of female. First antenna (Fig. 3g) approximately 225 μm long, 15-segmented, slightly modified. Lengths of segments (measured along their posterior nonsetiferous margins): 23 (42 μm along anterior margin), 18, 13, 6.5, 4.5, 5.5, 11, 15, 3, 26, 13, 10, 23, 28, and 33 μm, respectively. Formula for armature: 8, 3, 2, 2 + 1 aesthete, 2, 2, 2, 2, 2, 1, 2 + 1 aesthete, 2, 1, 3, and 8 + 1 aesthete. Second antenna as in female.

Labrum, mandible, first maxilla, second maxilla, maxilliped, and legs 1–4 as in female.

Leg 5 resembling that of female.

Leg 6 posteroventral flap on genital segment bearing 1 spiniform seta with slightly swollen base and 2 slender setae (Fig. 3f).

Spermatophore (Fig. 3h), attached to female, elongate 36 × 18 μm, not including neck.

Color unknown.

Etymology.—The specific name *verecunda,* Latin meaning modest or retiring, alludes to the moderately expressed features of this species.

Remarks.—*Euryte verecunda* resembles *E. bellatula* Humes, 1991, in several respects, such as body form, segmentation of the first antenna, structure of the second antenna, labrum, mouthparts, and legs 1–4, but differs from that species as in Table 1.

Additional measurements of the caudal ramus of six female paratypes of *E. bellatula* are: average 65 × 18 μm, ratio 3.61:1, range of length 61–73 μm.

Distinctions between *E. verecunda* and *E. bellatula* in some cases are more clearly ex-

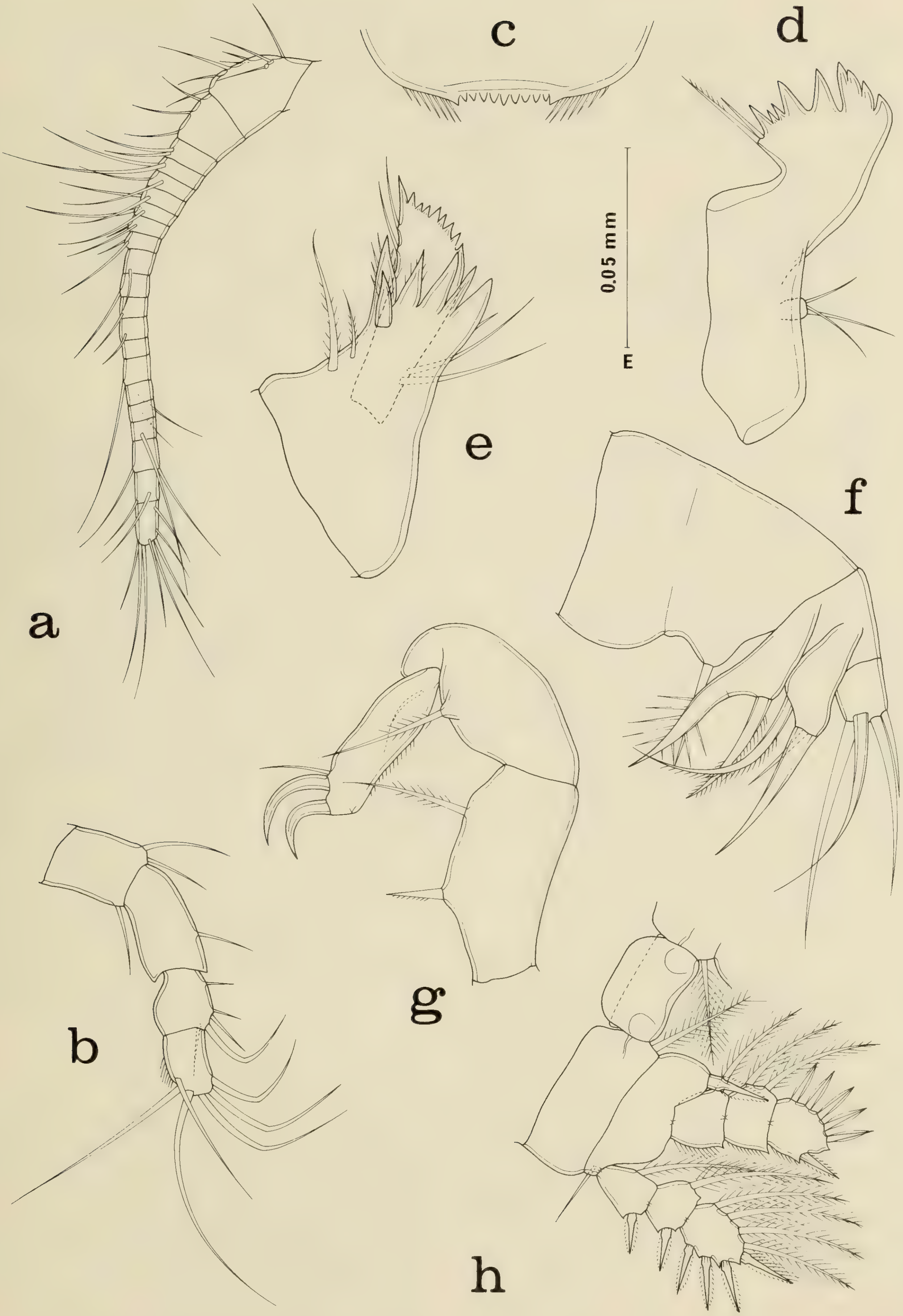

Fig. 2. *Euryte verecunda,* new species, female. a, first antenna, posteroventral (scale D); b, second antenna, antero-outer (D); c, posteroventral edge of labrum, ventral (D); d, mandible, inner (E); e, first maxilla, inner (E); f, second maxilla, outer (D); g, maxilliped, inner (E); h, leg 1 and intercoxal plate, anterior (D).

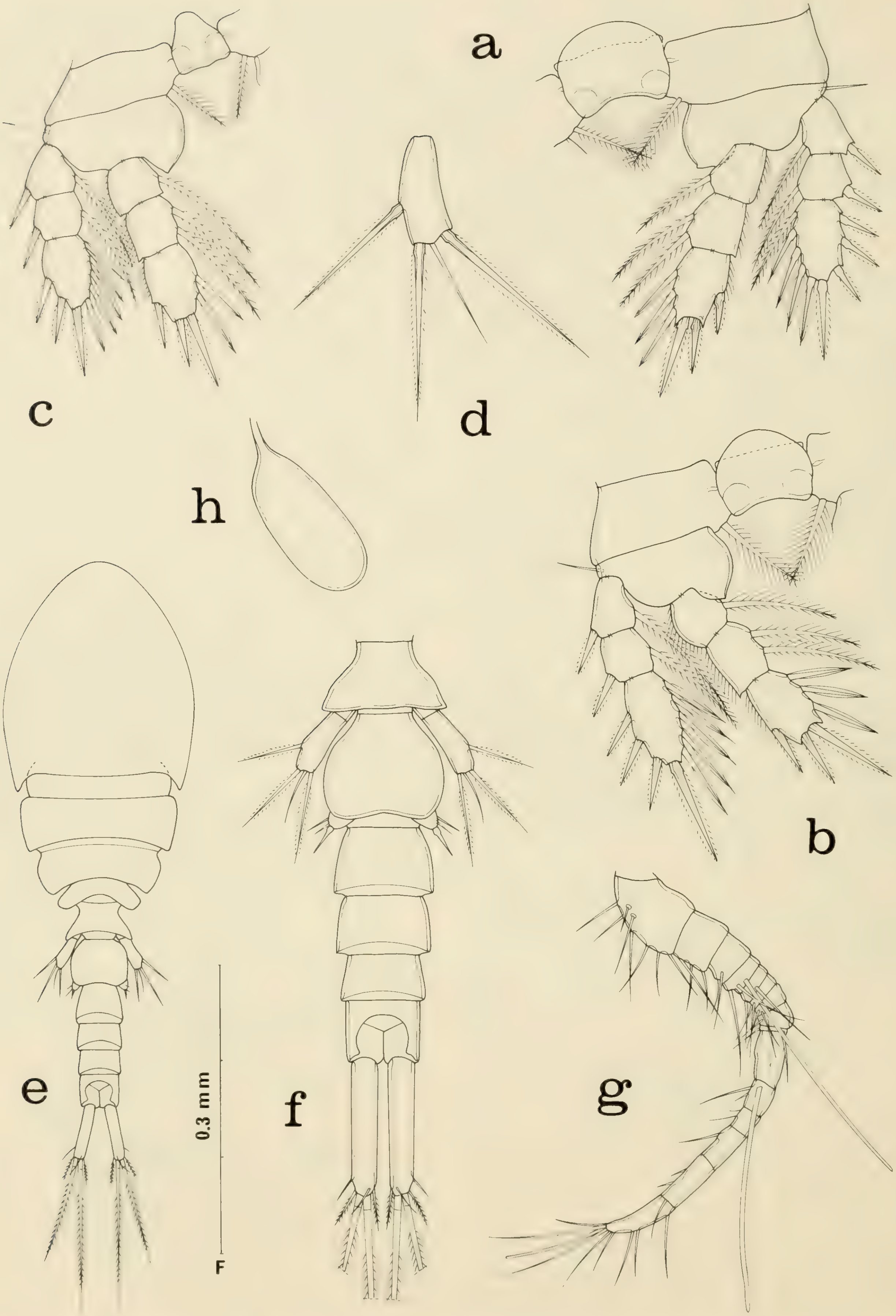

Fig. 3. *Euryte verecunda,* new species. Female: a, leg 2 and intercoxal plate, anterior (scale D); b, leg 3 and intercoxal plate, anterior (D); c, leg 4, anterior (D); d, second segment of leg 5, flat outer view (C). Male: e, dorsal view (F); f, urosome, dorsal (D); g, first antenna, ventral (D); h, spermatophore, attached to female, lateral (E).

Table 1.—Comparison of *Euryte bellatula* with *E. verecunda.*

	E. bellatula	*E. verecunda*
Length of body (♀) (mm)	0.83 (0.80–0.87)	0.77 (0.74–0.81)
Prosome, ratio of length : width (♀)	1.52:1	1.82:1
Caudal ramus, ratio of length : width (♀)	3.6:1	5.85–6.23:1
Ratio of length of caudal ramus to that of anal segment (♀)	1.64:1	1.93:1
Leg 4 exopod 3, ratio of length of terminal spine: adjacent outer spine (♀)	1.57:1 (55:35 μm)	1.90:1 (55:29 μm)
Host	*Montipora*	*Porites*

pressed by ratios rather than by absolute measurements. Careful study is necessary to distinguish these species, preferably involving a series of specimens. One feature of the new species that is of interest when compared with congeners is that in the new species and in *E. bellatula* the first antenna is 21-segmented, while in other species it has 20 or 21 segments, in one case 18 segments (Sars 1913, Scott 1912, Sewell 1949, Vervoort 1964).

Euryte verecunda is a frequent associate of *Porites lobata* in Panama. The copepod was found in considerable numbers on fragments of five different colonies of the coral. This is the second species of *Euryte* known to be coral-inhabiting, the first being *E. bellatula* associated with several species of *Montipora* in New Caledonia, on the Great Barrier Reef, and at Banda in the Moluccas (Humes 1991).

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NAUPLII AND COPEPODIDS OF THE CYCLOPOID COPEPOD *DIOITHONA OCULATA* (FARRAN, 1913) (OITHONIDAE) FROM A MANGROVE CAY IN BELIZE

Frank D. Ferrari and Julie W. Ambler

Abstract.—Somites, appendage segments and armament elements of 6 naupliar and 6 copepodid stages are described for *Dioithona oculata* (Farran, 1913) from Belize. *Dioithona oculata* were cultured on *Isochrysis galbana* from egg through naupliar stage 5 with some individuals growing as far as copepodid stage 3; copepodid stages were collected from daytime swarms. At 31°C, development time from 50% N1 to 50% N5 was 3.8 days. New information about morphological development is described for appendage segments and armament elements. Modified setae are present only on copepodids and are found on exopods of the mandible and maxillule, the endopod of swimming leg 4, and on the caudal ramus. The naupliar antennule is 2-segmented and the number of setae on this appendage is reduced from nauplius 6 to copepodid I. Development of ramal segments for swimming legs follows the common pattern for copepods with identical patterns for legs 1 and 2. The pattern of addition of setae and spines is identical for swimming legs 2 and 3. A study of formation homology for swimming leg 3 suggests that new segments form proximally to the distal-most segment of each ramus; new armament elements usually appear first at the proximal edge of the distal-most segment and subsequently become incorporated onto the next newly formed segment at the next molt.

Oithonid copepods are among the numerically dominant copepod species in many estuarine, coastal, and oceanic ecosystems (Marshall 1949, Marlowe & Miller 1975, Peterson et al. 1979, Lonsdale 1981, Turner & Dagg 1983, Ambler et al. 1985, Roman et al. 1985, Paffenhöfer et al. 1987). Some developmental stages of oithonid species have been described for nine species belonging to *Oithona* and one species of *Dioithona* (Table 1). No descriptions are available for the remaining oithonid genera, *Paroithona* and *Limnoithona*. From our studies of swarms of *D. oculata*, we describe changes in the exoskeletal morphology for all naupliar and copepodid stages, present molting rates for naupliar stages, compare our findings to developmental information known for other cyclopoid copepods, and discuss homologies of several appendages and their armament.

Dioithona oculata is a tropical cyclopoid copepod with a circumglobal distribution in neritic areas (Nishida 1985). During the day, *D. oculata* often forms swarms, composed of copepodid stages, in coral reef and mangrove habitats (Emery 1968, Hamner & Carlton 1979, Ueda et al. 1983, Ambler et al. 1991). Along mangrove shores of cays off Belize, swarms of *D. oculata* among mangrove roots disperse at sunset to open water 3–5 m away, adjacent to shore. Before dawn the copepodids move back under the mangroves to form swarms during the day (Ambler et al. 1991). Females produce egg sacs at night, and approximately 24 hours later, nauplii hatch to join the plankton in the water adjacent to the mangroves (Am-

Table 1.—Sources of information about development of cyclopod copepods.

Name	Source
Oithonidae	
Dioithona rigida	Ramamohana Rao (1958) [as *Oithona*]
Oithona atlantica	Gibbons & Ogilvie (1933) [as *O. spinirostris*]
O. brevicornis	Goswami (1975)
O. davisae	Uchima (1979) [as *O. brevicornis*]
O. nana	Haq (1965) [as *Oithonina*]
O. nana	Murphy (1923)
O. oligohalina	Fonseca & Almeida Prado (1979)
O. ovalis	Fanta (1976)
O. similis	Gibbons & Ogilvie (1933) [as *O. helgolandica*]
O. hebes?	Goswami (1975) [*O. hebes* is neotropical]
Ascidicolidae	
Ascidicola rosea	Illg & Dudley (1980)
Enterocola fulgens	Canu (1892)
E. fertilis	Illg & Dudley (1980)
E. laticeps	Illg & Dudley (1980)
Enteropsis capitulatus	Illg & Dudley (1980)
Haplosaccus elongatus	Ooishi (1980)
Haplostoma albicatum	Ooishi (1980)
Haplostomella distincta	Ooishi (1980)
H. oceanica	Ooishi (1980)
Zanclopus cephalodisci	Calman (1908)
Cyclopidae	
Acanthacyclops viridus	Lucks (1927) [as *Cyclops*]
Allocyclops silvaticus	Rocha & Bjornberg [in litt.]
Apocyclops dengizicus	Valderhaug & Kewalramani (1979)
Bryocyclops caroli	Bjornberg (1984)
Cyclops strenuus	Gurney (1932)
Diacyclops bicuspidatus	Amores-Serrano (1978) [as *Cyclops*]
Ectocyclops rubescens	Carvalho (1971)
Eucyclops serrulatus	Auvray & Dussart (1966)
Graeteriella unisetigera	Lescher-Moutoué (1973)
Halicyclops neglectus	Candeias (1966)
Macrocyclops albidus	Defaye (1984)
Mesocyclops edax	Amores-Serrano (1978)
Speocyclops racovitzai	Lescher-Moutoué (1966)
Cyclopinidae	
Cyclopina longifera	Goswami (1977)
Lernaeidae	
Lamproglena chinensis	Kuang (1962)
Lernaea cyprinacea	Grabda (1963)
Notodelphyidae	
Doroixys uncinata	Canu (1892)
Doropygus seclusus	Dudley (1966)
Notodelphys affinis	Dudley (1966)
Pachypygus gibber	Hipeau-Jacquotte (1978)
Pygodelphys aquilonaris	Dudley (1966)
Scolecodes huntsmani	Dudley (1966)

bler et al. 1990). Nauplii remain in the plankton until they molt to the first copepodid stage (CI); CI's migrate horizontally to swarms among mangrove roots. Two other oithonid species are present with *D. oculata* in the plankton at night. *O. fonsecae* is found in tropical Atlantic lagoonal waters (Ferrari & Bowman 1980), and *O. nana* has a tropical oceanic and nearshore distribution (Nishida 1985).

Methods

Copepodid stages of *D. oculata* were sorted from preserved swarm samples collected at Twin Cays, Belize (16°50′N, 88°05′W), in May 1985, June 1988, and July 1990. Nauplii were cultured from eggs hatched from dropped egg sacs of females isolated from swarm samples collected in February and May 1989. Nauplii were kept in several 500 ml (February) or 50 ml (May) beakers of ambient seawater which were suspended with a styrofoam float in a water-bath cooler, and fed a chrysomonad, *Isochrysis galbana.* Temperatures varied from 20–25°C in February and 30–31°C in May. In February, 12–80 nauplii from several beakers were collected daily; during May, 30–70 nauplii were collected from a 50 ml beaker in 8–12 hr intervals. Specimens were fixed with 2.0% formaldehyde, preserved in 0.5% propylene phenoxytol/4.5% proplylene glycol/95.0% water, cleared in steps through 50.0% lactic acid/50.0% water to 100% lactic acid, and stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% water.

Table 2.—Development of *Dioithona oculata* nauplii reared in laboratory from May 18, 1989 experiment. Time from egg hatching to 50% of stage i (T50), instar duration (T), coefficient of determination (R2) for linear regression of angular transformed percent stage versus time. In parentheses is probability of rejecting Ho: Slope = 0, Slope, and Intercept. *n* = number of points in regression.

Stage	*n*	T_{50} (hours)	T (hours)	R^2	Slope	Intercept
N1	4	24.00	10.93	0.959 (0.0206)	0.225	−4.62
N2	3	34.93	34.89	1.000 (0.0105)	0.125	−3.57
N3	8	69.82	25.00	0.901 (0.0003)	0.0274	−1.13
N4	8	94.82	21.22	0.744 (0.0059)	0.0250	−1.59
N5	8	116.04	—	0.767 (0.0043)	0.0167	−1.15

Depending upon their availability, up to 30 specimens of each stage were measured to determine body length; caudal rami were included in body length measurements of copepodids. From 3 to 10 specimens of each stage were dissected; the number depended upon the degree of difficulty in determining structural morphology or variability of an appendage. Results consist of brief descriptions of changes in each appendage for each developmental stage. The ventral view of nauplii or lateral view of copepodids are shown for each developmental stage, and the appropriate appendages are illustrated. Descriptions of appendage segments or their armament elements are not repeated if they have not changed from the previous stage. Dense setules on a seta or spine are indicated in illustrations only over a short section of a seta and are not repeated for similar elements.

Developmental times for naupliar stages were determined from the experiment started on May 18, 1989. The time when 50% of the nauplii had molted to a particular stage was determined from linear regression of the angular transformation (Sokal & Rohlf 1969) of percent stage as a function of time. Developmental times were calculated as a difference of times between two successive stages for 50% of the specimens to molt. The angular transformation for each stage, which is the arcsine of the square root of the percent molted to the next stage, was used to meet the assumption of constant variance. Time was calculated from time zero (May 18, 0400) when females produce egg sacs (see Ambler et al. 1990).

Naupliar stages are abbreviated N1 to N6; copepodid stages CI to CVI; male = m, female = f. Appendages are A1 = antennule; A2 = antenna; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla; Mxp = maxilliped; swimming legs = legs 1–4; posterior to these are two simple appendages = legs 5 and 6; caudal ramus = CR. Appendage segments are named following Boxshall (1985) with exopods = Re; endopods = Ri; medial lobes of a segment = li. Armament elements of appendages are spines and setae which are distinguished by apparent degree of flexibility (Dudley 1966); medial, terminal and lateral elements are si, st and se. Homology of appendages, their segments and elements in different developmental stages usually was established by position and occasionally by morphology. For a few appendages, homology by formation was determined if the developing appendage or element of a succeeding stage was visible within the skeleton of the preceding stage.

Results

For experiments in February and May 1989, *D. oculata* was reared from N1

Table 3.—Length range (mm), number of somites or complexes [two or more fused somites] (S + C), appendage buds and number of swimming legs (S1) on stages of *Dioithona oculata*. *n* = number of specimens.

Stage	*n*	Range	S + C	Buds	S1
N1	20	0.11–0.13	1	0	0
N2	18	0.12–0.14	1	0	0
N3	12	0.12–0.14	1	0	0
N4	10	0.15–0.16	1	mx1	0
N5	7	0.16–0.17	1	mx1	0
N6	20	0.19–0.21	1	mx1, legs1,2	0
CI	20	0.34–0.37	6	leg3	2
CII	20	0.39–0.42	7	leg4	3
CIII	30	0.43–0.49	8	leg5	4
CIV	30	0.52–0.60	9	legs5,6	4
CV	30	0.59–0.67	10	leg6	4
CVIf	30	0.73–0.80	10	leg6	4
CVIm	30	0.64–0.70	11	leg6	4

through CIII on unialgal cultures of *Isochrysis galbana*. During February when temperatures varied between 20–25°C, CI were present 8–11 days after egg hatching. In May, sufficient nauplii were raised at nearly constant temperature (30–31°C) to calculate development times for the first four naupliar stages (Table 2). N1 had the shortest development time (10.93 hr) and N2 the longest (34.89 hr). Durations of N3 and N4 were approximately one day. When the experiment was terminated 7.2 days after egg hatching, 56% of the animals had molted to at least N6, and 23% were copepodids.

There are 6 naupliar and 6 copepodid stages of *D. oculata*. Body length and somite number are given in Table 3 and Figs. 1A, E, 2A, D, 3A, E, 4A, 5A, 6A, 7A, 8A, E, and 9E. In N1–5 all cephalic somites are fused into a single complex segment; in N6 this complex includes the first 3 thoracic somites. In CI–CVI all cephalic and the first thoracic somites are fused into a complex, and in addition in CVIf the seventh thoracic and first abdominal somites are fused laterally and ventrally into a genital complex.

Posterior Armament and CR.—N1–N2 (Fig. 1A, E) 1 pair of setae. N3–N4 (Fig. 2A, D) 3 pairs of setae. N5–N6 (Fig. 3A, E) 5 pairs. CI CR (Fig. 4B) length 1.6× width, 1 lateral, 1 dorsal, 4 terminal setae; medialmost terminal seta with thick base and recurved medially. CII–CIII (Fig. 5B) no setae recurved. CIV–CV (Fig. 7B) length 1.8× width. CVIf (Fig. 8F) length 2.5× width. CVIm (Fig. 10E) length 2.0× width.

A1.—[* = count includes a small, pointed seta; a = count includes an aesthetasc] N1–N2 (Fig. 1B) 2 segments with 3 and 4 setae. N3 (Fig. 2B) segment 2 with 7 setae. N4 (Fig. 2E) segment 2 with 12 setae. N5 (Fig. 3B) segment 1 with 4 setae, segment 2 with 14 setae. N6 (Fig. 3F) segment 2 with 16 setae. CI (Fig. 4C) 4 segments with 3, 3, 1 and 9 setae. CII (Fig. 5C) 7 segments with 3, 3, 2, 1, 1, 1 and 10 setae. CIII (Fig. 6B) 9 segments with 3, 3, 2, 3, 4, 1, 2, 2, and 11 setae. CIV (Fig. 7C) 11 segments with 2, 3, 6, 3*, 4, 4, 2a, 3, 2, 3 and 7a setae. CV (Fig. 8B) 11 segments with 7, 8, 3, 4*, 4, 4, 2a, 3, 2, 3, and 7a setae. CVIf (Fig. 10A) 11 segments with 2, 5, 10, 6*, 4, 4, 2a, 3, 2, 3, and 7a setae. CVIm (Fig. 10F) 15 segments with 2, 5, 4, 3, 2, 2, 1, 1, 1, 2, 2, 2, 3, 2, and 9aa setae plus 3 sensilla.

A2.—N1 (Fig. 1C) coxa 2 si; basis 2 si; Re1 fused to basis; several indistinct segments and 6 setae; Ri1 4 setae. N2 (Fig. 1F) basis 3 si; Re 7 setae. N3 (Fig. 2C) coxa 3 si; Re 8 setae; Ri1 5 setae. N4 (Fig. 2F) Re 10 setae; Ri1 7 setae. N5 (Fig. 3C) Re 10 setae. N6 (Fig. 3G) Ri1 8 setae. CI (Fig. 4D) coxa and basis fused 2 si; Re1 wrinkled, 2 setae; Ri 10 setae. CII–CIII (Fig. 5D) Re 1 seta; Ri1 5 setae; Ri2 6 setae. CIV–CVIf (Fig. 6G) Ri2 7 setae. CVIm (Fig. 10G) Ri all segments more elongate.

Mn.—N1 (Fig. 1D) coxa 1 si; basis 2 si; Re1 1 si; Re2 1 si; Re3 2 setae; Ri1 2 si; Ri2 4 si. N2–N6 (Fig. 1G) Re3 1 si; Re4 1 st; Ri1 4 si. CI (Fig. 4E) coxa a gnathobase; basis 1 si; Re4 2 setae, lateral seta a brush; Ri1 fused with basis, 2 si; Ri2 4 setae. CII–CV (Fig. 5E) Ri2 5 setae. CVIf (Fig. 9A) Re4 1 si; Re5 1 seta a brush. CVIm (Fig. 9F) Ri1 2 setae; Ri2 5 setae.

Mx1.—N2–N3 (Figs. 1E, 2A) 1 seta, N4

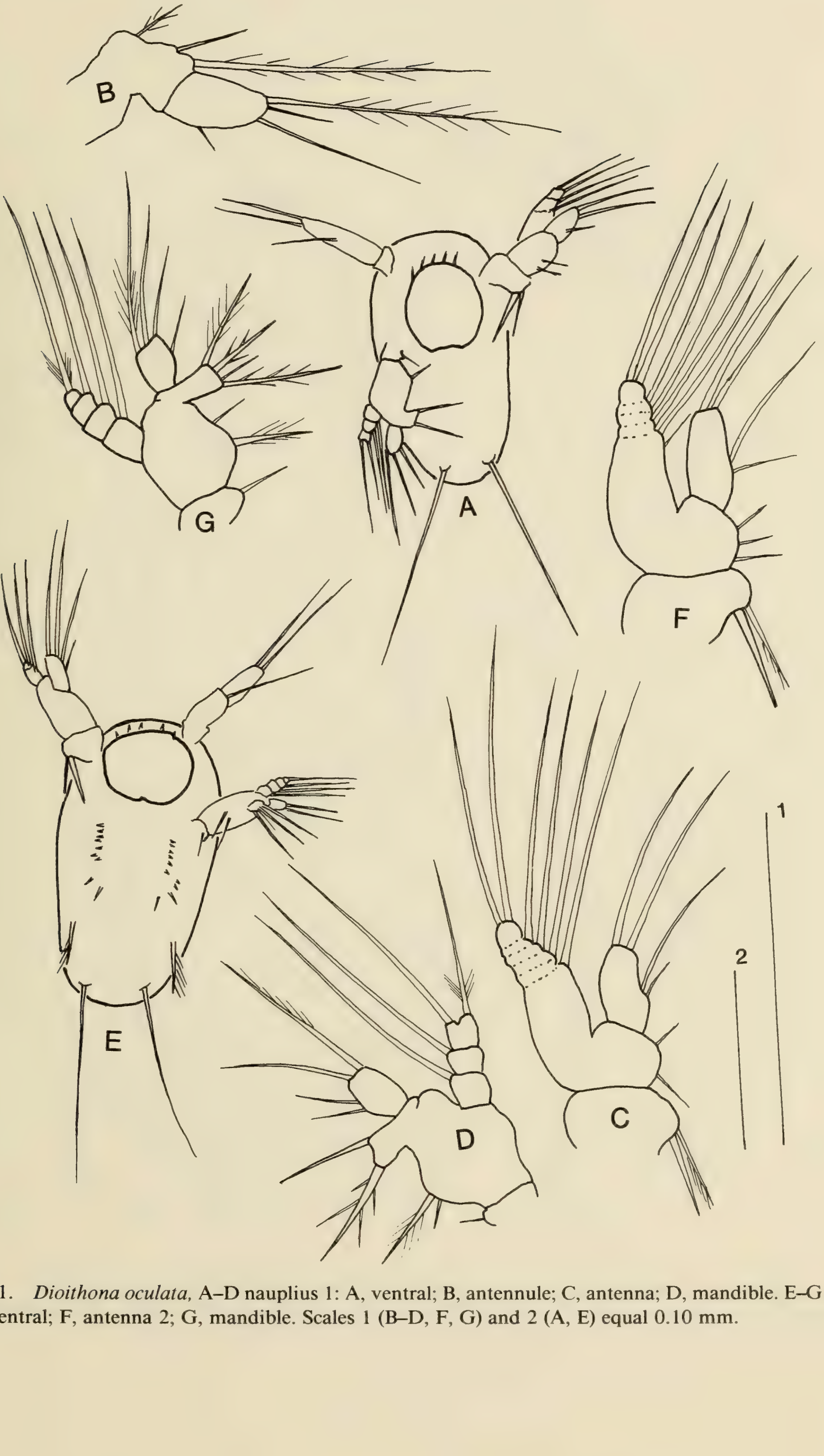

Fig. 1. *Dioithona oculata,* A–D nauplius 1: A, ventral; B, antennule; C, antenna; D, mandible. E–G nauplius 2: E, ventral; F, antenna 2; G, mandible. Scales 1 (B–D, F, G) and 2 (A, E) equal 0.10 mm.

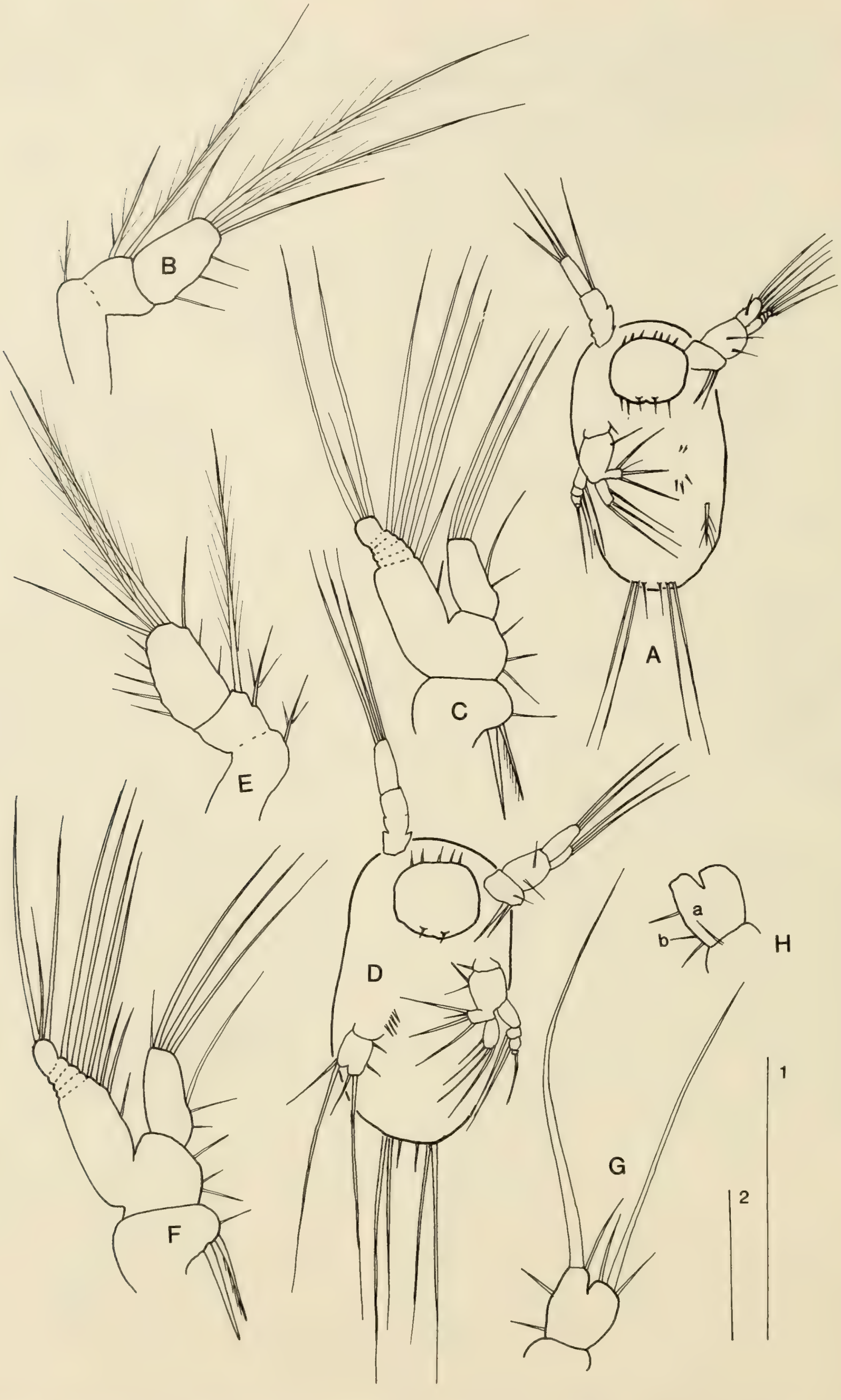

Fig. 2. *Dioithona oculata,* A–C nauplius 3: A, ventral; B, antennule; C, antenna. D–H nauplius 4: D, ventral; E, antennule; F, antenna; G, maxillule; H, maxillule variations (a = seta on 40% of May 1988 specimens and b = seta on one May 1988 specimen). Scales 1 (B, C, E–H) and 2 (A, D) equal 0.10 mm.

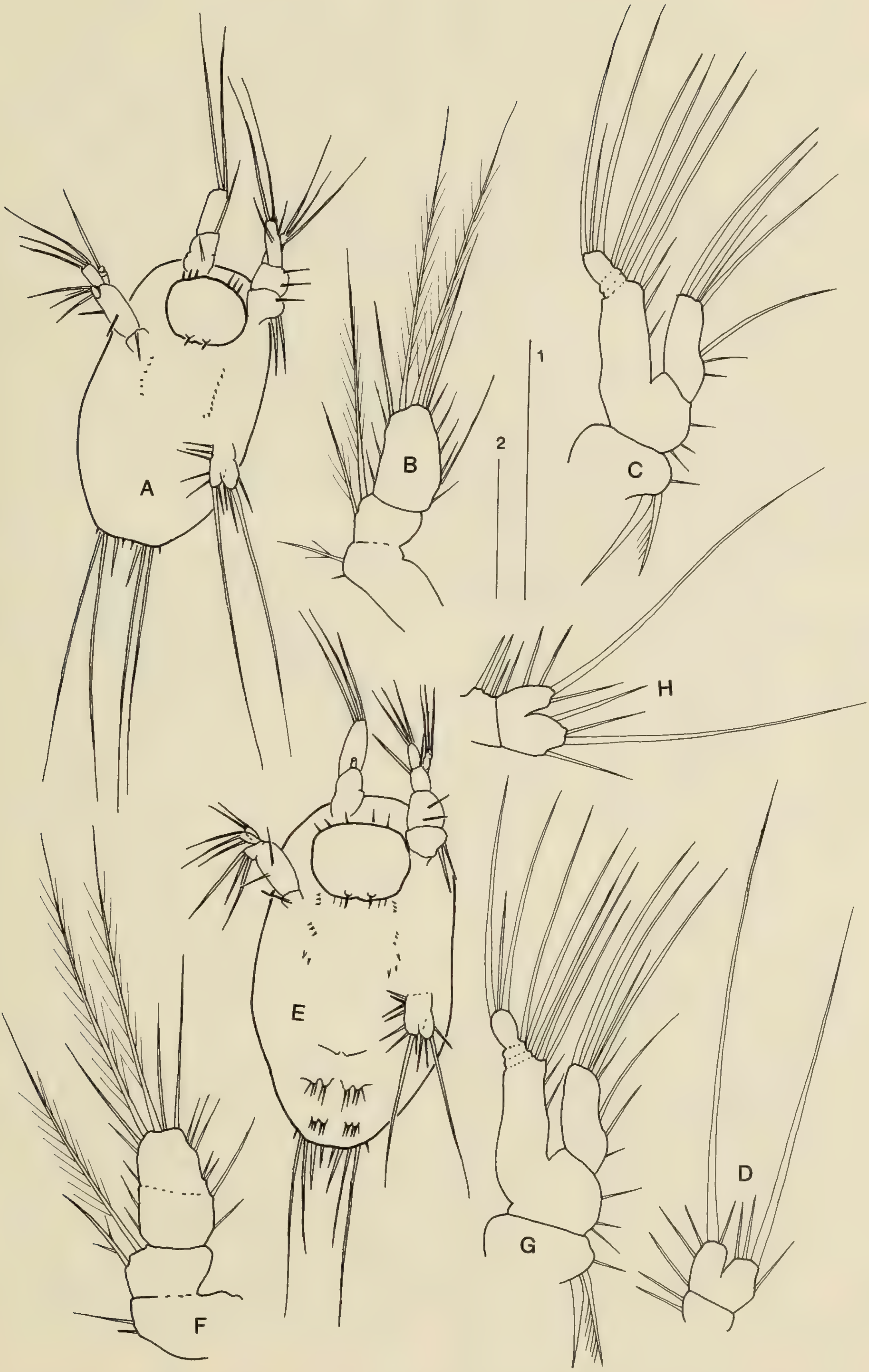

Fig. 3. *Dioithona oculata,* A–D nauplius 5: A, ventral; B, antennule; C, antenna; D, maxillule. E–H nauplius 6: E, ventral; F, antennule; G, antenna; H, maxillule. Scales 1 (B–D, F–H) and 2 (A, E) equal 0.10 mm.

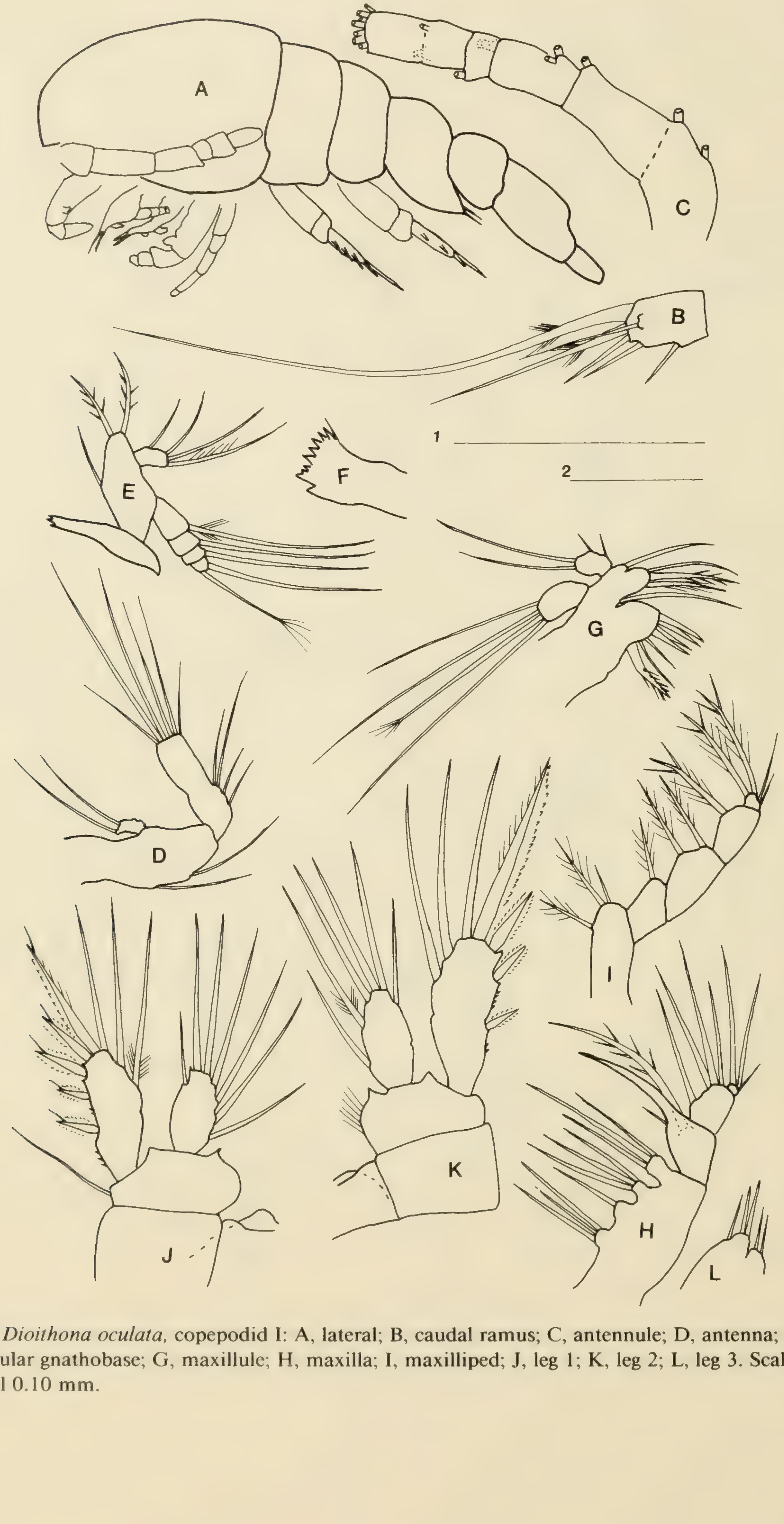

Fig. 4. *Dioithona oculata,* copepodid I: A, lateral; B, caudal ramus; C, antennule; D, antenna; E, mandible; F, mandibular gnathobase; G, maxillule; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 3. Scales (B–L) and 2 (A) equal 0.10 mm.

(Fig. 2G) a bilobed bud with basal segment; le 3 setae, li 4 setae [4 of 10 May specimens with an extra seta on basal segment; 1 other May specimen with li 5 setae]. N5 (Fig. 3D) basal segment 2 Si, le 4 setae; li 5 setae. N6 (Fig. 3H) basal segment 3 si. CI–CII (Fig. 4G) sympod li1 7 setae, li2 1 setae, li3 3 setae, li4 1 setae; Re1 4 setae, 2nd seta a brush; Ri1 4 setae, CIII-CVI (Figs. 6H, 9C) sympod li1 9 setae.

Mx2.—CI (Fig. 4H) coxa li1 3 setae, li2 1 seta, li3 3 setae, li4 3 setae; basis with distal inner corner elongate as a curved claw, 2 si; Ri1 4 si; Ri2 3 setae. CII–CV (Fig. 7H) Ri2 2 setae; Ri3 3 setae. CVIf (Fig. 11A) Ri2 3 setae; Ri3 4 setae. CVIm (Fig. 11C) Ri2 5 setae.

Mxp.—CI–CII (Fig. 4I) praecoxa 3 si; coxa 1 si; basis 2 si; Ri1 1 si; Ri2 4 setae. CIII (Fig. 6C) praecoxa 4 si; coxa 2 si; Ri1 2 si. CIV–CVI (Fig. 9D, H) syncoxa 6 si; basis 2 si and inner row of hairs; Ri1 3 setae.

Leg 1.—N6 (Fig. 3E) a bilobed bud le 3 setae, li 2 setae. CI (Fig. 4J) coxa naked; basis 1 se; Re1 with 4 se, 3 si, 1 st; Ri1 7 setae. CII (Fig. 5F) coxa 1 si; basis 1 si; Re1 1 se; Re2 3 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIII-CIV (Fig. 6I) Re1 1 se, 1 si; Re2 3 se, 4 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVIf (Fig. 10B) Rel 1 se, 1 si; Re2 1 se, 1 si; Re3 3 se, 4 si, 1 st; Ri1 1 si; Ri2 1 si; Ri3 6 setae. CVIm (Fig. 9I) basis 1 si recurved medially.

Leg 2.—N6 (Fig. 3E) a bilobed bud le 3 setae, li 2 setae. CI (Fig. 4K) coxa naked; basis naked; Re1 with 3 se, 3 si, 1 st; Ri1 6 setae. CII (Fig. 5G) coxa 1 si; basis 1 se; Re1 1 se; Re2 2 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIII–CIV (Fig. 6J) Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVI (Fig. 10C) Re1 1 se, 1 si; Re1 1 se, 1 si; Re3 3 se, 5 si, 1 st; Ri1 1 si; Ri2 2 si; Ri3 6 setae.

Leg 3.—CI (Fig. 4L) a bilobed bud le 3 setae, li 2 setae. CII (Fig. 5H) coxa naked; basis naked; Re1 with 3 se, 3 si, 1 st; Ri1 6 setae. CIII (Fig. 6D) coxa 1 si; basis 1 se; Re1 1 se; Re2 2 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIV (Fig. 7D) Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVI (Fig. 10D) Re1 1 se, 1 si; Re2 1 se, 1 si; Re3 3 se, 5 si, 1 st; Ri1 1 si; Ri2 2 si; Ri3 6 setae.

Leg 4.—CII (Fig. 5I) a bilobed bud le 3 setae, li 2 setae. CIII (Fig 6E) coxa naked; basis naked; Re 1 segment with 3 se, 3 si, 1 st, Ri 1 segment with 6 setae. CIV (Fig. 7E) coxa 1 si; basis 1 se; Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 6 setae. CV (Fig. 7G) Re1 1 se, 1 si; Re2 1 se, 1 si; Re3 2 se, 5 si, 1 st. CVIf (Fig. 11B) Ri2 both and Ri3 proximal setae modified, slightly curved distally with hyaline flange along inner edge. CVIm (Fig. 11D) Ri2 both and Ri3 proximal setae modified, straight with hyaline flange smaller than in female.

Leg 5.—CIII (Fig. 6F) unilobed bud with 2 setae. CIV (Fig. 7F) bilobed bud with 3 setae. CV–CVI (Figs. 8D, H, 9J) basal lobe with 1 seta; 1 segment with 2 setae.

Leg 6.—CIV–CVIm (Figs. 7F, 8D, 9K) unilobed bud with point and 1 seta. CVIf (Fig. 8H) unilobed bud with seta recurved dorsally.

Discussion

Our specimens of *D. oculata* differ from those (as *Oithona oculata*) of Nishida (1985) in the following: (1) A1 of our females has two fewer segments; apparently our 3rd and 6th segments represent fused segments (Fig. 10A); (2) Mxp of the female has one fewer segment (Fig. 9D), i.e., praecoxa and coxa are fused, and medial spinules at base of segment 1 are absent; (3) modified setae on female and male Mn, Mx 1, leg 4, and male leg 1 are present (Figs. 9A, C, F, 10F, K). We believe that these modified setae are difficult to discern and may have been overlooked in earlier studies. Ferrari & Bowman (1980) described modified setae (previously noted for *O. plumifera* by Giesbrecht 1892, and for *O. brevicornis* and *O. hebes* by Wel-

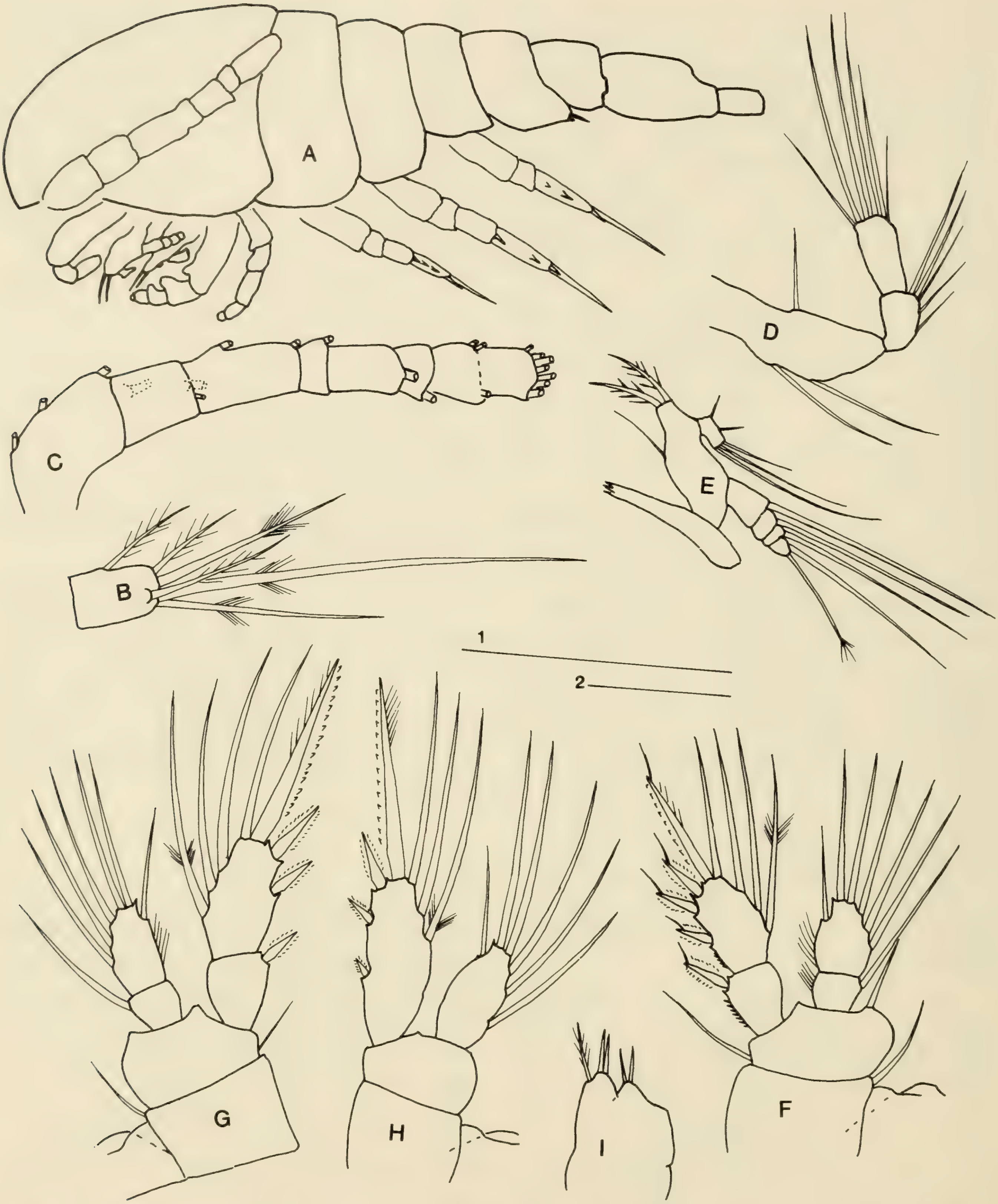

Fig. 5. *Dioithona oculata,* copepodid II: A, lateral; B, caudal ramus; C, antennule; D, antenna; E, mandible; F, leg 1; G, leg 2; H, leg 3; I, leg 4. Scales 1 (A) and 2 (B–I) equal 0.10 mm.

lershaus 1969) on leg 4 of many *Oithona* females, including *D. oculata,* but failed to detect these setae on males of *D. oculata.*

Oithonid species (*O. nana, O. similis, O. brevicornis, O. hebes*?, *O. colcarva,* and *O. davisae*) have been cultured on diets of chlorophyte flagellates, dinoflagellates, and chryptophyte flagellates (Haq 1965, Eaton

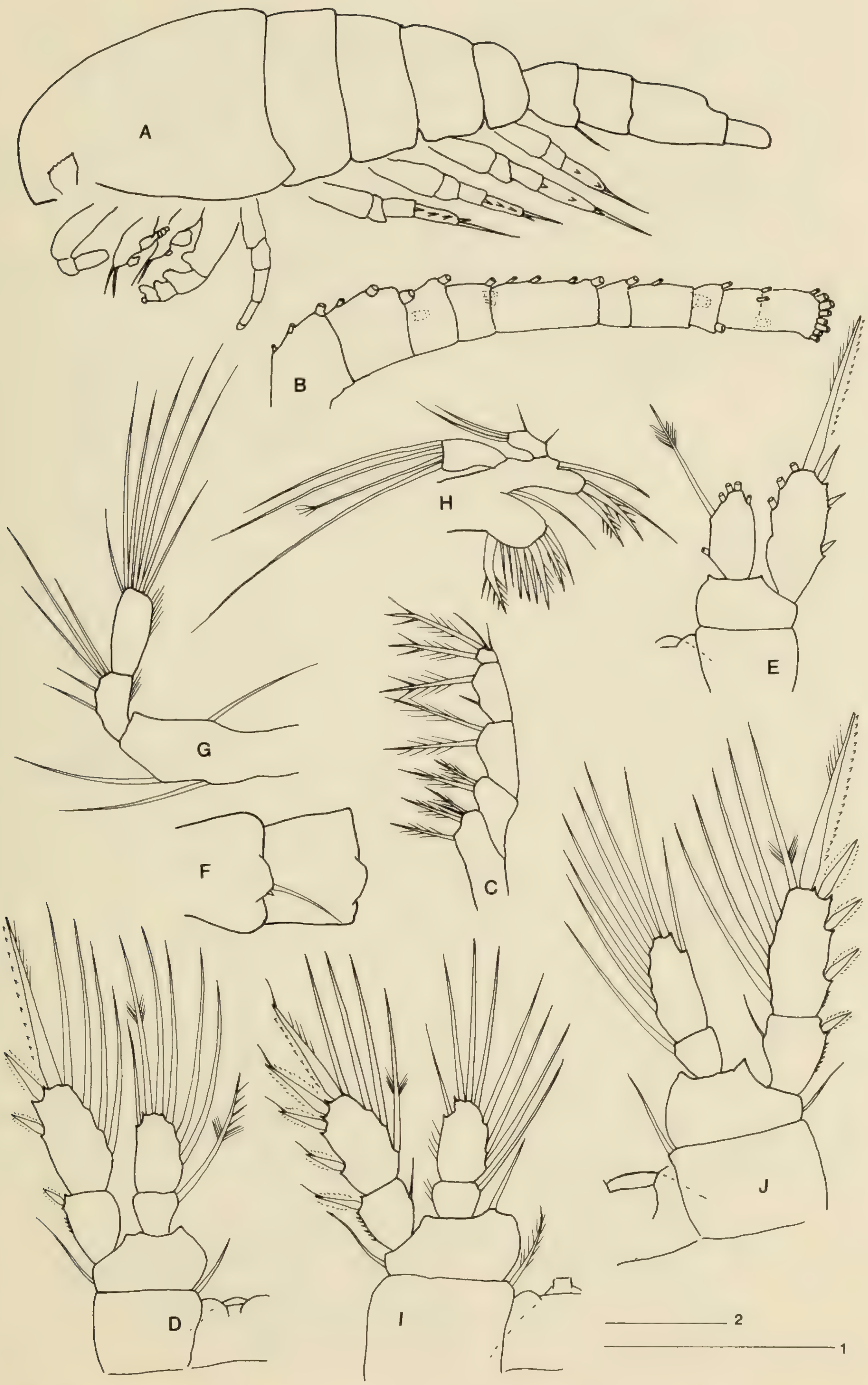

Fig. 6. *Dioithona oculata,* A–F copepodid III: A, lateral; B, antennule; C, maxilliped; D, leg 3; E, leg 4; F, leg 5. G–J copepodid IV: G, antenna; H, maxillule; I, leg 1; J, leg 2. Scales 1 (B–J) and 2 (A) equal 0.10 mm.

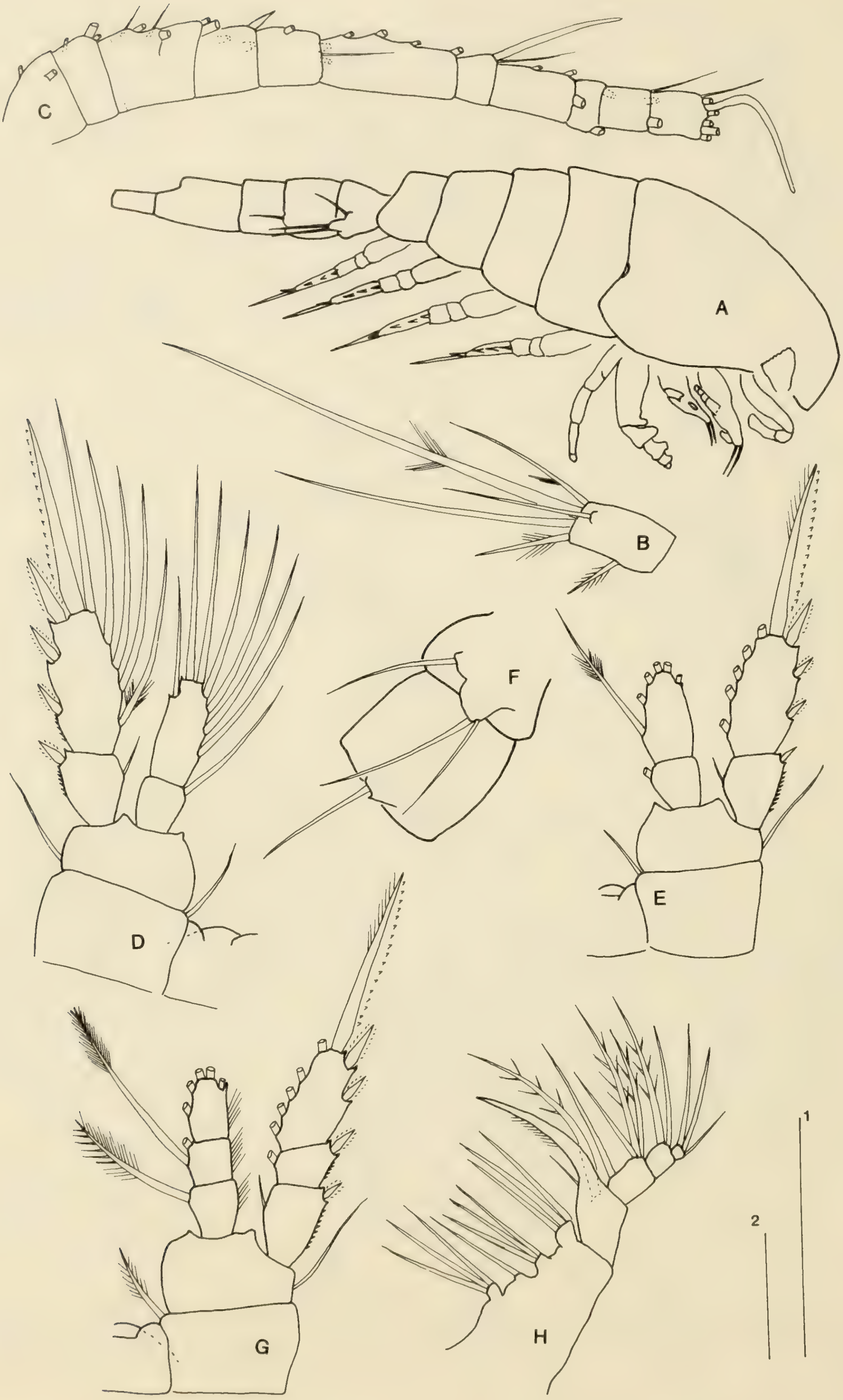

Fig. 7. *Dioithona oculata,* A–F copepodid IV: A, lateral; B, caudal ramus, C, antennule; D, leg 3; E, leg 4; F, legs 5–6. G–H copepodid V: G, leg 4; H, maxilla. Scales 1 (B–H) and 2 (A) equal 0.10 mm.

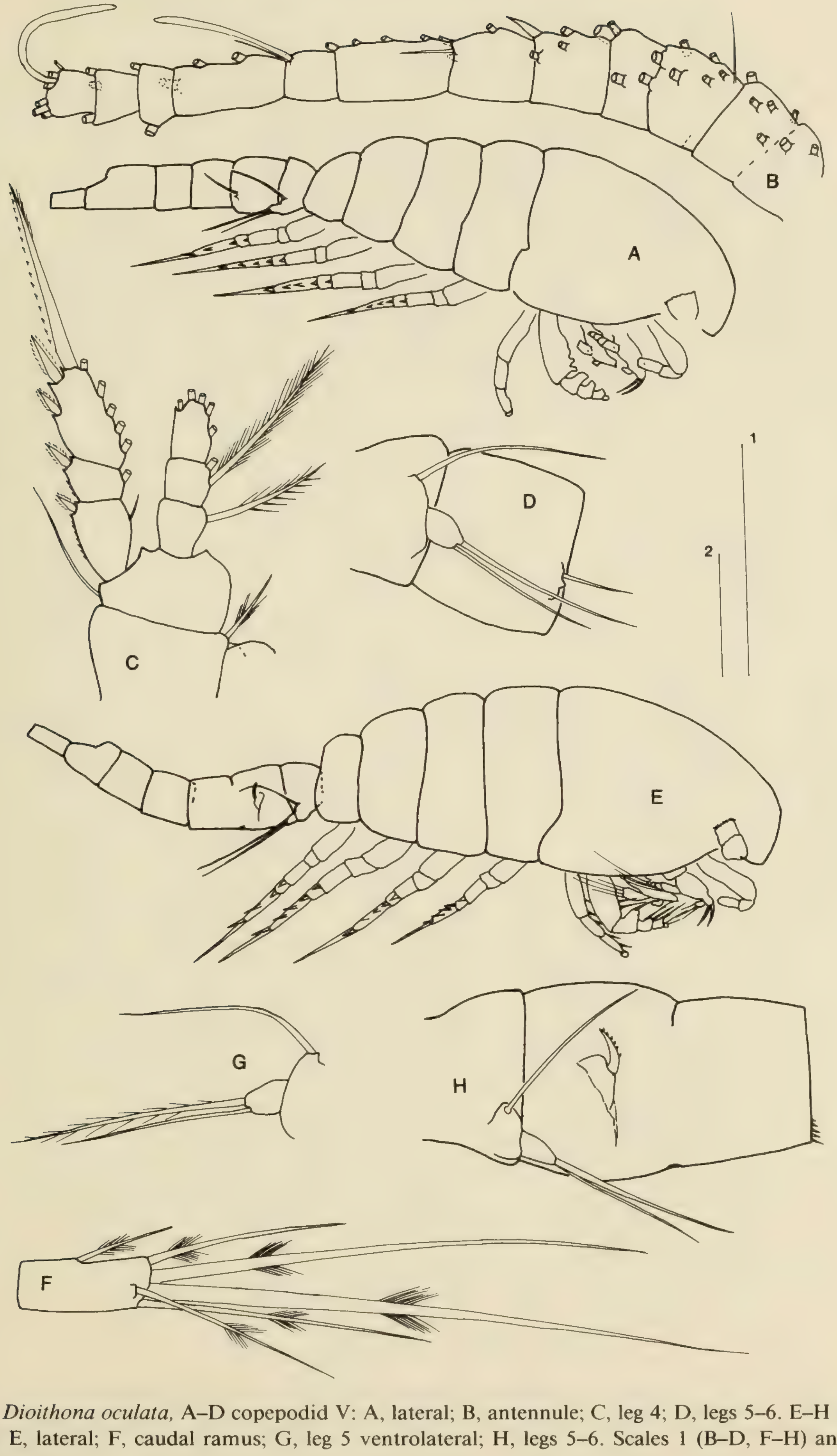

Fig. 8. *Dioithona oculata,* A–D copepodid V: A, lateral; B, antennule; C, leg 4; D, legs 5–6. E–H copepodid VI female: E, lateral; F, caudal ramus; G, leg 5 ventrolateral; H, legs 5–6. Scales 1 (B–D, F–H) and 2 (A, E) equal 0.10 mm.

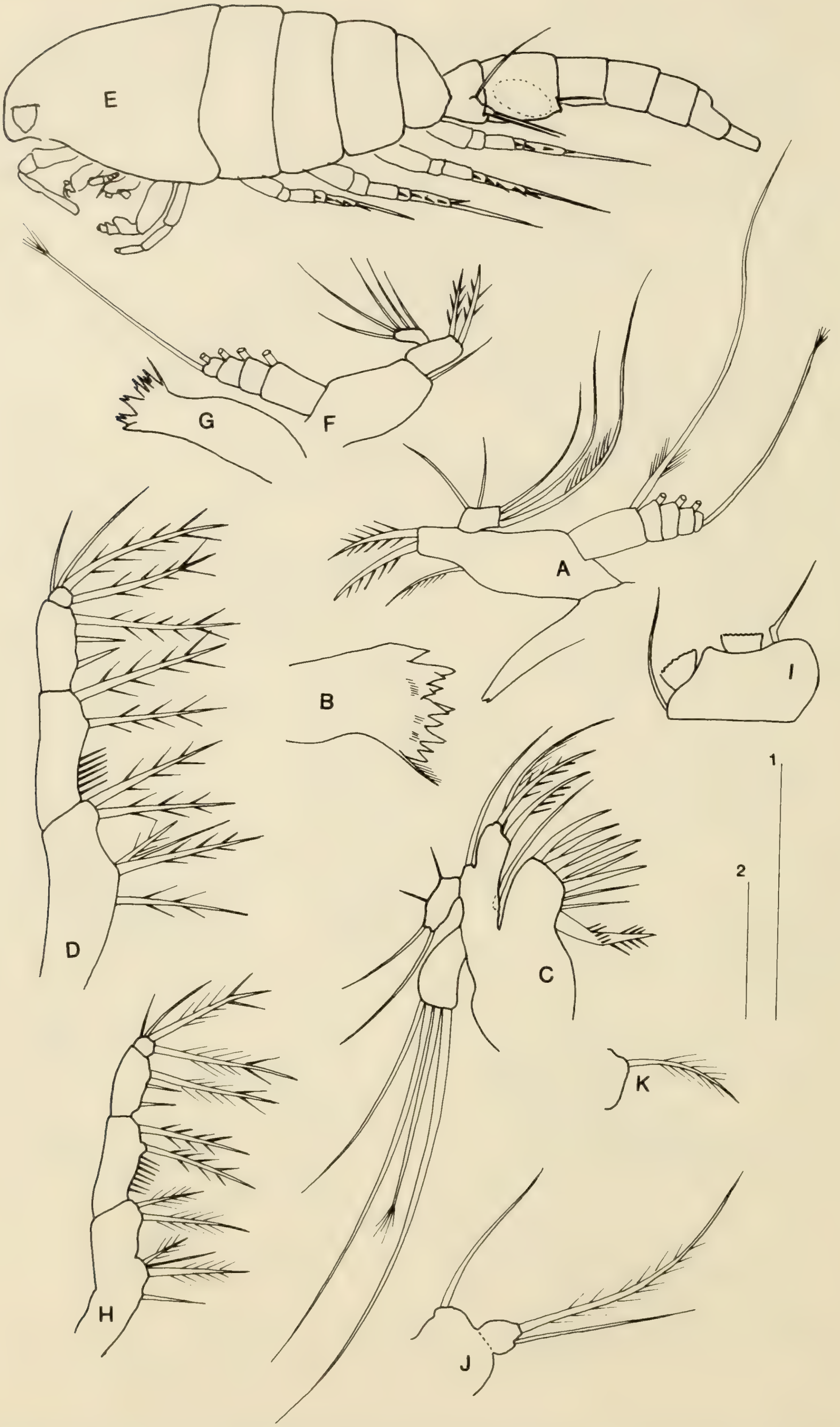

Fig. 9. *Dioithona oculata,* A–D copepodid VI female: A, mandible; B, mandibular blade; C, maxillule; D, maxilliped. E–K copepodid VI male: E, lateral; F, mandible; G, mandibular blade; H, maxilliped; I, leg 1 basis; J, leg 5; K, leg 6. Scales 1 (A–D, F–K) and 2 (E) equal 0.10 mm.

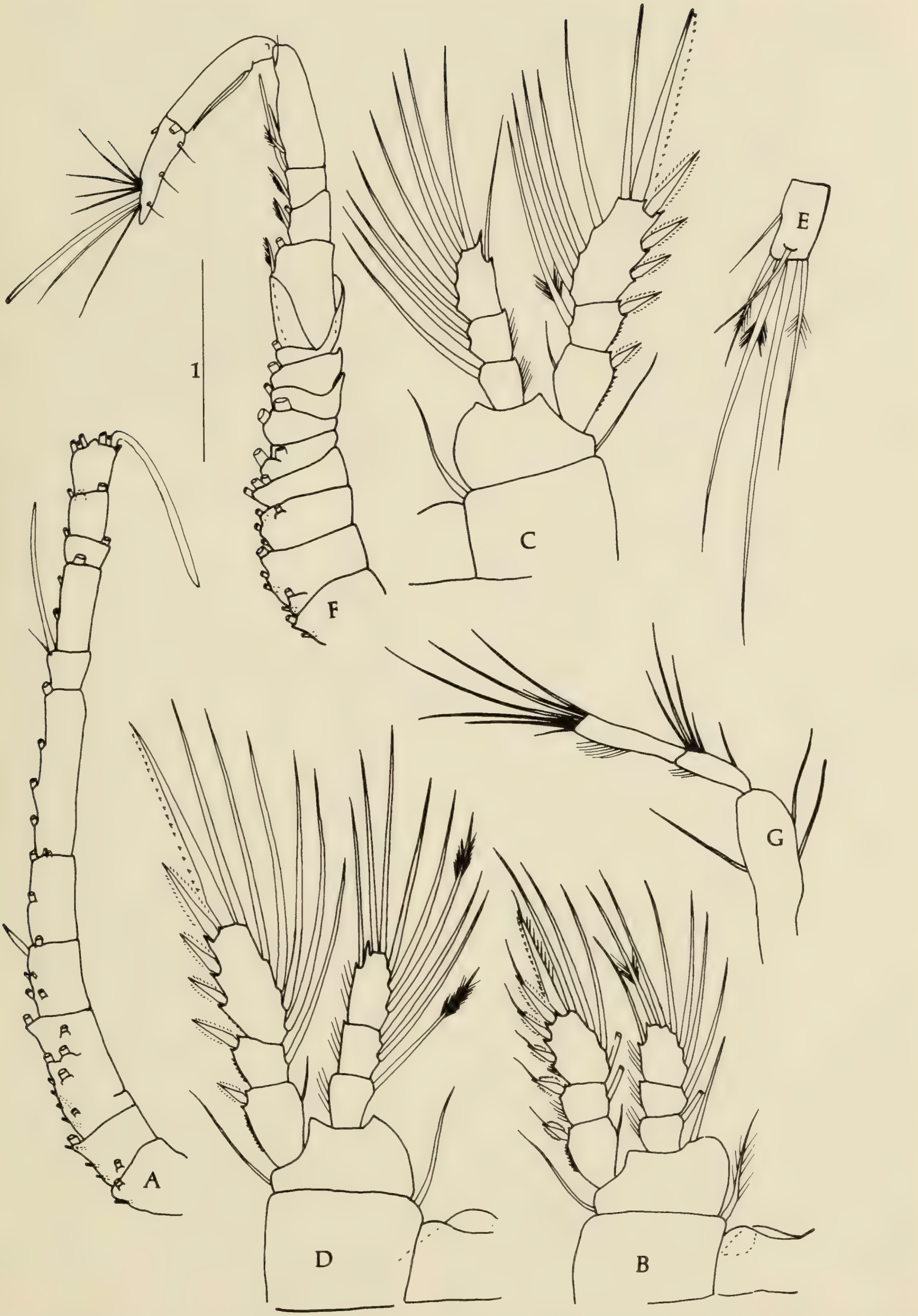

Fig. 10. *Dioithona oculata,* A–D copepodid VI female: A. antennule; B, leg 1; C, leg 2; D, leg 3. E–G copepodid VI male: E, caudal ramus; F, antennule; G, antenna. Scale 1 equals 0.10 mm.

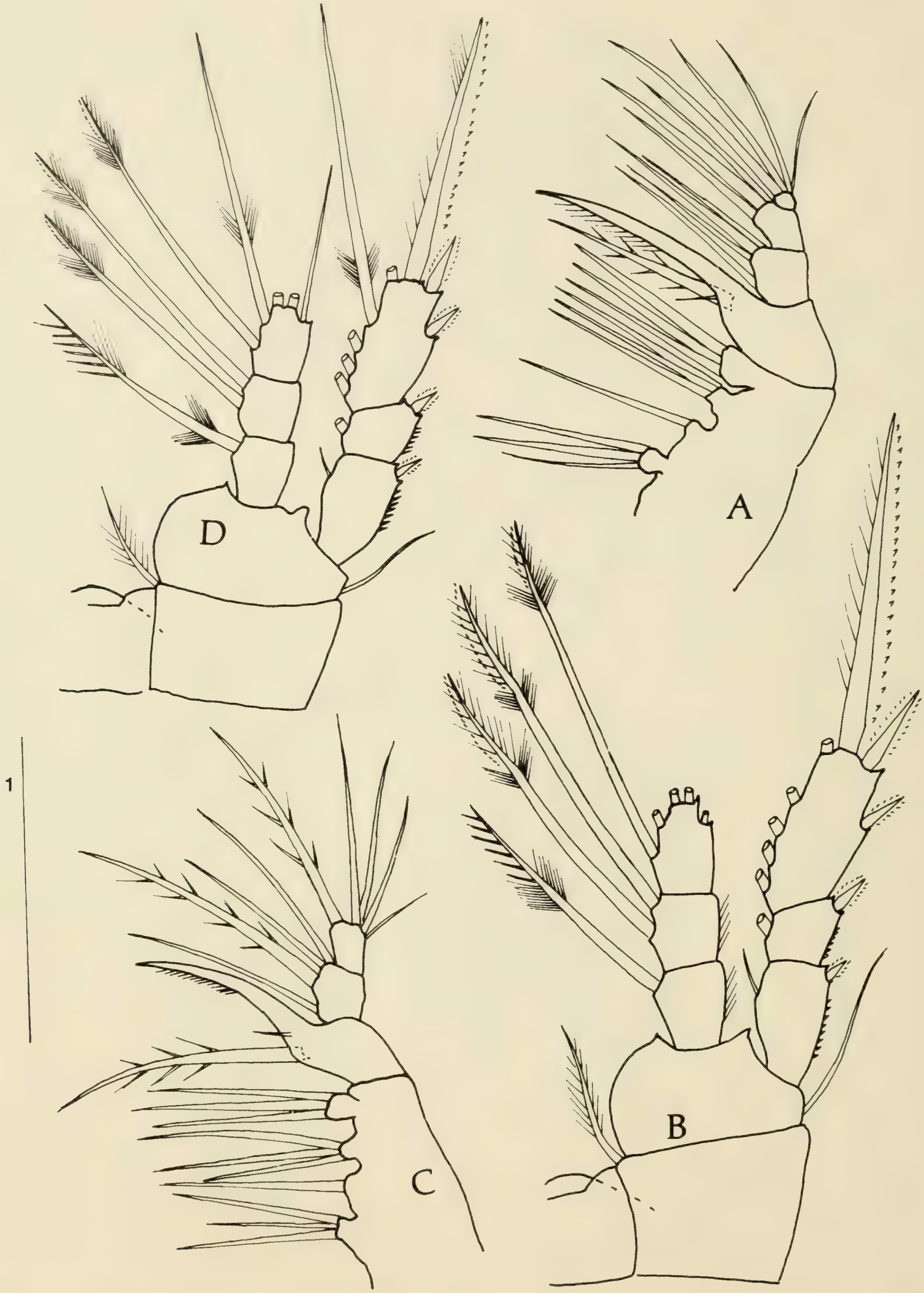

Fig. 11. *Dioithona oculata,* A–B copepodid VI female: A, maxilla; B, leg 4. C–D copepodid VI male: C, maxilla; D, leg 4. Scale 1 equals 0.10 mm.

1971 referenced in McLaren (1978), Goswami 1975, Lonsdale 1981, Uchima 1979). Protozoans such as oligotrichines are ingested by all stages of *O. davisae* (Uchima & Hirano 1986), and Murphy's (1923) kelp detritus for *O. similis* included protozoans. Diatoms are not as readily ingested by oithonids, but several species (*O. similis, O. nana,* and *O. davisae*) have been reported to ingest at least one species (Murphy 1923, Haq 1965, Uchima & Hirano 1986). *Isochrysis galbana* was sufficient for growth for most of the naupliar stages of *D. oculata* but growth of N5 and N6 may have been retarded. Growth of older nauplii and copepodids probably depends on diets of larger protists such as the dinoflagellate *Amphidinium klebsii,* which was fed to adult females for egg production (unpublished data). Females did not produce new egg sacs when offered other species such as newly hatched *Artemia salina,* the rotifer *Asplancha* sp., and *Dunaliella salina.* Older nauplii and copepodids may also need larger food species.

The first feeding stages varies with copepod species, but it is usually the naupliar stage of longest duration (Landry 1983). For *O. similis* and *O. davisae,* N1 is the first feeding stage (Uchima & Hirano 1986). Orange droplets, probably yolk, were observed in the guts of N1 of *D. oculata*; its first feeding stage is probably N2 because it is the naupliar stage of longest duration (Table 3).

The development time for growth between egg hatching and CI has been determined for several oithonid species with varying precision. For most published studies it is difficult to determine from methods if time from N1 to CI is the time to the first appearance of CI, or to the time of 50% CI which is used in the present study. Development time as a function of temperature (Fig. 12), however, shows a classical Beléhrádek function which has been observed for egg development rates (McLaren 1966). Goswami (1975) determined that *O. brevicornis* and *O. hebes*? developed from N1 to CI in 8–10 and 10–14 days, respectively, at 24–27°C. Several species of calanoid copepods raised at 15°C developed from hatching to CI in 6.5–9.8 days (Landry 1983), which was much faster than oithonid species (Fig. 12). Development time for *D. oculata* to 50% N5 was 3.83 days, and development to 50% CI probably is in the range of the other oithonid species. Since ambient temperatures near the Belizean mangroves are typically near 30°C, *D. oculata* probably is adapted to growth at maximal rates at these high temperatures.

Dioithona oculata possesses a 2-segmented naupliar A1 (Figs. 1B, 2B, E, 3B, F), a brush-like seta on the exopod of both Mn and Mx1 of all copepodids (Figs. 4E, F, 5E, 6H, 9A, C, F), and modified setae on the basis of the male leg 1 (Fig. 9I). These structures have not been described for other cyclopoid copepods. A reduction (from 20 to 16) of setae on A1 from N6 to CI (Figs. 3F, 4C) has been reported only for *O. similis* and *O. atlantica.* Presence on male leg 4 of three endopodal setae modified with a hyaline flange similar to female leg 4 is unique to *D. oculata* (Fig. 11B, D).

Development of exopodal and endopodal segments of the swimming legs of *D. oculata* follows the common pattern described by Ferrari (1988, 1991) with the segmentation pattern of legs 1 and 2 identical, while legs 3–6 are similar but one copepodid stage each out of register. The addition of armament elements to each ramus is a more complex process. Six conditions of appendage development (Table 4) can be defined: (A) a leg bud, (B) a reorganized swimming leg with 1-segmented exopod and endopod, (C) an early 2-segmented exopod and endopod, (D) a later 2-segmented exopod and endopod, (E) a final 2-segmented exopod and endopod, (F) a 3-segmented exopod and endopod. Conditions A–F occur in legs 1–2, conditions A–D, and F occur in leg 3, and conditions A, B, D, and F occur in leg 4. Addition of armament elements on legs 1–

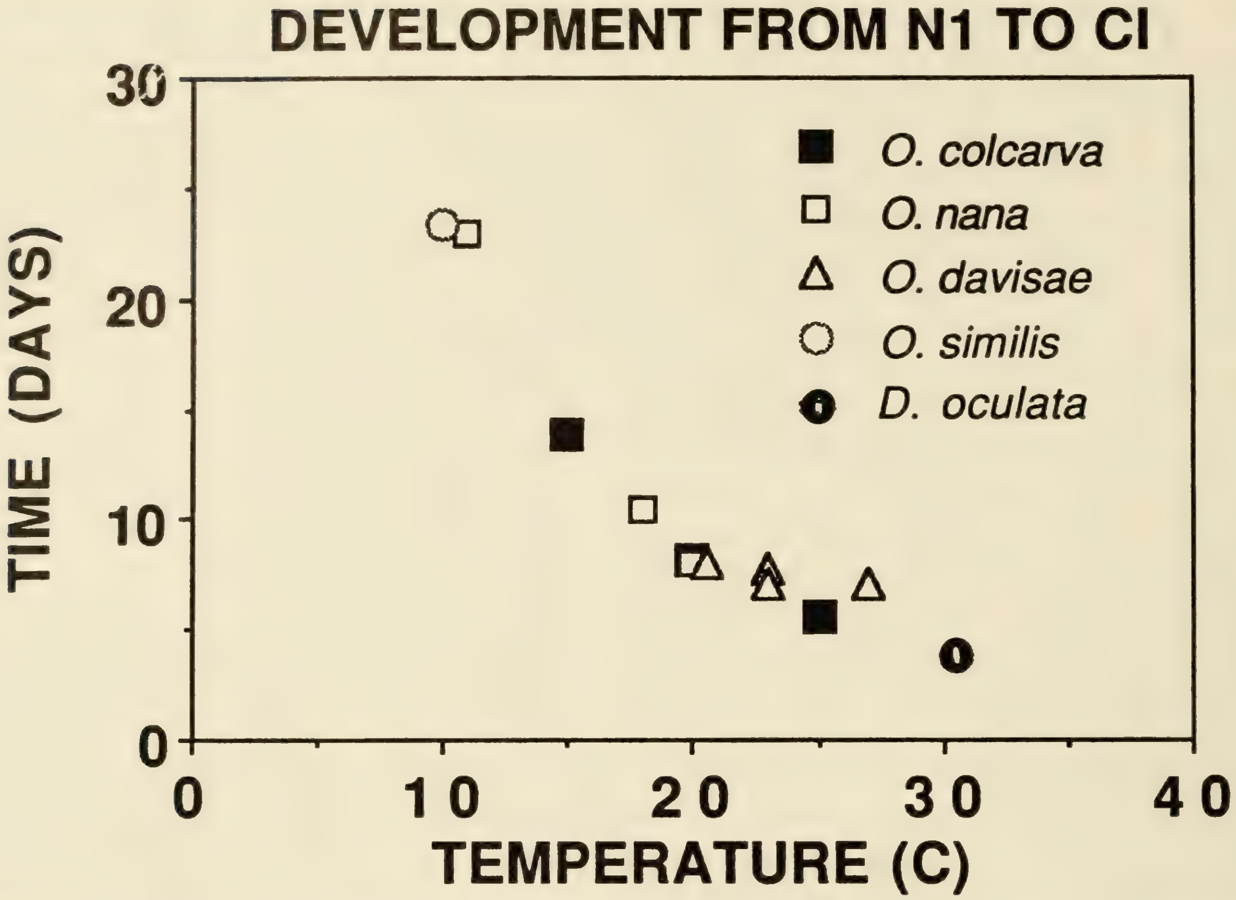

Fig. 12. Development time (days) as a function of temperature from egg hatching to CI for oithonid species. Only mean values are plotted. When means are not given, the middle value of the range is plotted. Literature values of development time given as mean and standard deviation (*O. colcarva* by Lonsdale 1981), mean and range (*O. davisae* by Uchima and Hirano 1986), range (*O. davisae* by Uchima 1979), range (*O. nana* by Haq 1965), and overall mean and range of means (*O. similis* by Eaton 1971 as referenced in McLaren 1978). *Dioithona oculata* development time from 50% N1 to 50% N5 from Table 3. Standard deviation or range from means was 1.2 at most, except for *O. similis* with a range of 2.0.

3 occurs prior to conditions B, C, D, and F. Addition of elements for leg 4 occurs prior to conditions in B, D, and F.

For swimming legs 2 and 3, identical numbers of elements are present on the exopod and endopod segments for each leg condition (Table 4). For leg 1 there are more elements present early in development and fewer present later in development than for legs 2 and 3. We have assumed that the early 2-segmented condition (condition C) is skipped for leg 4 so that numbers of exopodal elements are identical to legs 2 and 3 but the endopod of leg 4 has fewer elements later in development.

Inferences about homologies of several appendages of *D. oculata* can be drawn from the development of their segments by comparing morphology, position, or formation. Homology by morphology suggests that the Re1 of naupliar A2 is fused to the basis, and that the medial recurved seta of CR on CI may become the second from medial seta on CR of CII–CVI.

In *D. oculata* the elongate lateral extension of the basis of A2 (e.g., Fig. 1C) is a fused exopodal segment, and not an extension of the basis as has been described as a part of the basis for *Haplosaccus elongatus, Doropygus seclusus, Notodelphys affinis, Pygodelphys aquilonaris,* and *Scolecodes huntsmani,* because several inner setae are added to it in later naupliar stages (Fig. 3G). Armament additions such as this have not been reported for the basis of other copepod appendages. In most descriptions of cyclo-

Table 4.—Number of armament elements for *Dioithona oculata* of the exopod (Re) and endopod (Ri) of legs 1–4. Six leg conditions: (A) leg bud, (B) reorganized swimming leg with 1-segmented exopod and endopod, (C) early 2-segmented exopod and endopod, (D) later 2-segmented exopod and endopod, (E) final 2-segmented exopod and endopod, (F) 3-segmented exopod and endopod are listed on the left; the number of setae plus spines present on each ramus are given to the left of the slash and the stage of development is given to the right. C = copepodid; n = nauplius; nc = no change from previous stage in number of elements; np = condition not present for that leg.

	Leg Re				Leg Ri			
Leg condition	1	2	3	4	1	2	3	4
bud	3/n6	3/n6	3/CI	3/CII	2/n6	2/n6	2/CI	2/CII
1 + 1	8/CI	7/CI	7/CII	7/CIII	7/CI	6/CI	6/CII	6/CIII
2 + 2 (early)	9/CII	8/CII	8/CIII	np	7/CII	7/CII	7/CIII	np
2 + 2 (late)	10/CIII	11/CIII	11/CIV	11/CIV	8/CIII	8/CIII	8/CIV	7/CIV
2 + 2 (final)	nc/CIV	nc/CIV	np	np	nc/CIV	nc/CIV	np	np
3 + 3	12/CV	13/CV	13/CV	13/CV	8/CV	9/CV	9/CV	8/CV

poid naupliar development, a similarly elongate Re1 articulates with a simple, unextended basis. Other cyclopoid species in which this segment is described correctly as fused include *Ascidicola rosea* and *Lernaea cyprinacea.*

The long, thick, recurved, medial seta on the distal edge of the CR of CI (Fig. 4B) of *D. oculata* may be the homologue of the long, thick, second-from-medial seta of CII (Fig. 5B). A distinctively modified medial seta like that of *D. oculata* also is known for CI of *Haplosaccus elongatus, Haplostoma albicatum,* and *Lernaea cyprinacea.* Like *D. oculata,* CII of the first two species has a small, simple medial seta, and a longer thicker, second-from-medial seta. In CII–VI of *L. cyprinacea,* a distinctively modified seta of similar morphology to the modified medial seta of CI is present at the second-from-medial position. The medial seta in CII–VI is small and simple. Given these morphological data, an hypothesis that the medial seta of CI is the homologue of the second-from-medial seta in CII–VI of *D. oculata* seems reasonable. The identity of the seta on CI that is homologous to the medial seta on CII remains unresolved, although Dahms (1990) has described the transposition of two setae in similar positions during the development of an harpacticoid copepod.

Homology by position suggests that the endopod of Mxp is 2-segmented in all copepodids of *D. oculata,* and that the mandibular Ri1 is fused to the basis except in CVI male in which it is an articulating segment.

In determining homologies for the 5-segmented Mxp of CI–II (Fig. 4I) of *D. oculata,* we compared the position of groups of medial setae to similarly positioned groups of *Archimisophria discoveryi* (Boxshall 1985: fig. 34). Boxshall reviewed various proposed segment homologies of copepod postmandibular appendages and, basing his argument on the origin and insertion of muscles, he designated the proximal two segments of Mx2 and Mxp, each with two setiferous lobes, as the praecoxa and coxa. Based on positions of similar setal groups, we have interpreted segmental homologies for Mxp of *D. oculata* as a praecoxa, coxa, basis and a 2-segmented endopod. Although praecoxa and coxa are fused later in development (Fig. 9D), the endopod of *D. oculata* remains 2-segmented throughout its development, an inference which supports Ho's (1986) description of the oithonid maxilliped.

The mandible of the CVI male of *D. oculata* possesses two articulating endopodal segments, while the first of these segments is fused to the basis in all other nauplii and copepodids (Figs. 2G, 4E). Homologies of mandibular segments are somewhat problematical; Izawa (1987) has suggested that the naupliar mandible of all cyclopoids has a 2-segmented endopod and a basis without medial lobes. Applying this definition, Ri1 (Fig. 2G) of *D. oculata* is fused to the mandibular basis, so that Ri1 with its two to four prominant spines forms a distal medial lobe of the basis. The articulating segment is Ri2. In CI the second mandibular segment is comprised of the basis and fused Ri1 with only two of the four prominent naupliar spines remaining; the articulating segment is Ri2. This condition also is found in CII–V and CVI female (Fig. 9A). We believe that an alternate hypothesis, i.e., that the naupliar inner lobe is a true lobe of the basis and not the fused Ri2, provides no unambiguous interpretation of the two free segments of CVI male.

Itô (1989) hypothesized that the basis of copepod appendages originated by fusions of proximal segments of the exopod and endopod. Our information about fusion of Re1 of A2 and Ri1 of Mn of *D. oculata* supports that hypothesis.

Homology by formation suggests that the outer seta on segment 1 of A2 on CII–CVI is the remnant of the naupliar exopod, and that the addition of segments and armament of leg 3 usually occurs proximally on the distal-most segment.

We observed seven specimens of N6 with a small, wrinkled lobe bearing two setae which was visible within the long, fused Re1 of the nauplius. We believe that the wrinkled lobe is the exopod of CI. In a specimen of CI, we observed the proximal section of a single, outer seta on segment 1 of the antennal exopod of CII which had formed within the wrinkled-lobe exopod of CI. However, we could not determine in which one of the terminal distal setae of CI the distal section of this seta of CII seta was formed. This seta is the homologue of an exopodal seta and the seta is a remnant in copepodids of the naupliar exopod.

Lucks (1927), Hulsemann & Fleminger (1975), and Hulsemann (1991b) have used formation homology during copepodid development, rather than positional or morphological homology, to determine segment or setal homologies of copepod appendages. We used this method to determine the fate of swimming leg armament elements. Our findings are illustrated in Fig. 13. We studied three specimens of CI in which the reorganized leg 3 of CII was visible within the leg 3 bud of CI, and one specimen of CII in which the reorganized leg 4 of CIII was visible within the leg 4 bud of CII. From these specimens we infer that the three setae on the outer lobe of these leg buds become the distal-most outer spine, the terminal spine and the distal-most inner seta of the exopod (Fig. 13B); two outer spines and two inner setae are newly added. Two setae on the inner lobe of the leg bud become the middle two of six setae on the endopod; one terminal seta, the outer seta, and two proximal inner seta are new.

We studied one specimen of CII in which leg 3 of CIII was present within leg 3 of CII. The new segment of both exopod and endopod formed proximally to the distal ramal segment (Fig. 13C). On this new exopodal segment is the older, proximal-most, outer spine, and on the new endopodal segment is the older, proximal-most, inner seta. New setae of CIII not formed within a seta of CII are the inner seta of the coxa, outer seta of the basis, and the proximal-most, inner seta on each distal ramal segment.

We examined two specimens of CIII in which leg 3 of CIV was visible within leg 3 of CIII. No new segments are added but the proximal-most, inner seta of the distal segment of the endopod and proximal-most, inner seta and outer spine of the distal segment of the exopod were not formed within an element of CIII. These elements are presumed new (Fig. 13D).

We studied one specimen of CIV in which leg 3 of CV was present within leg 3 of CIV. The new segment on each ramus formed

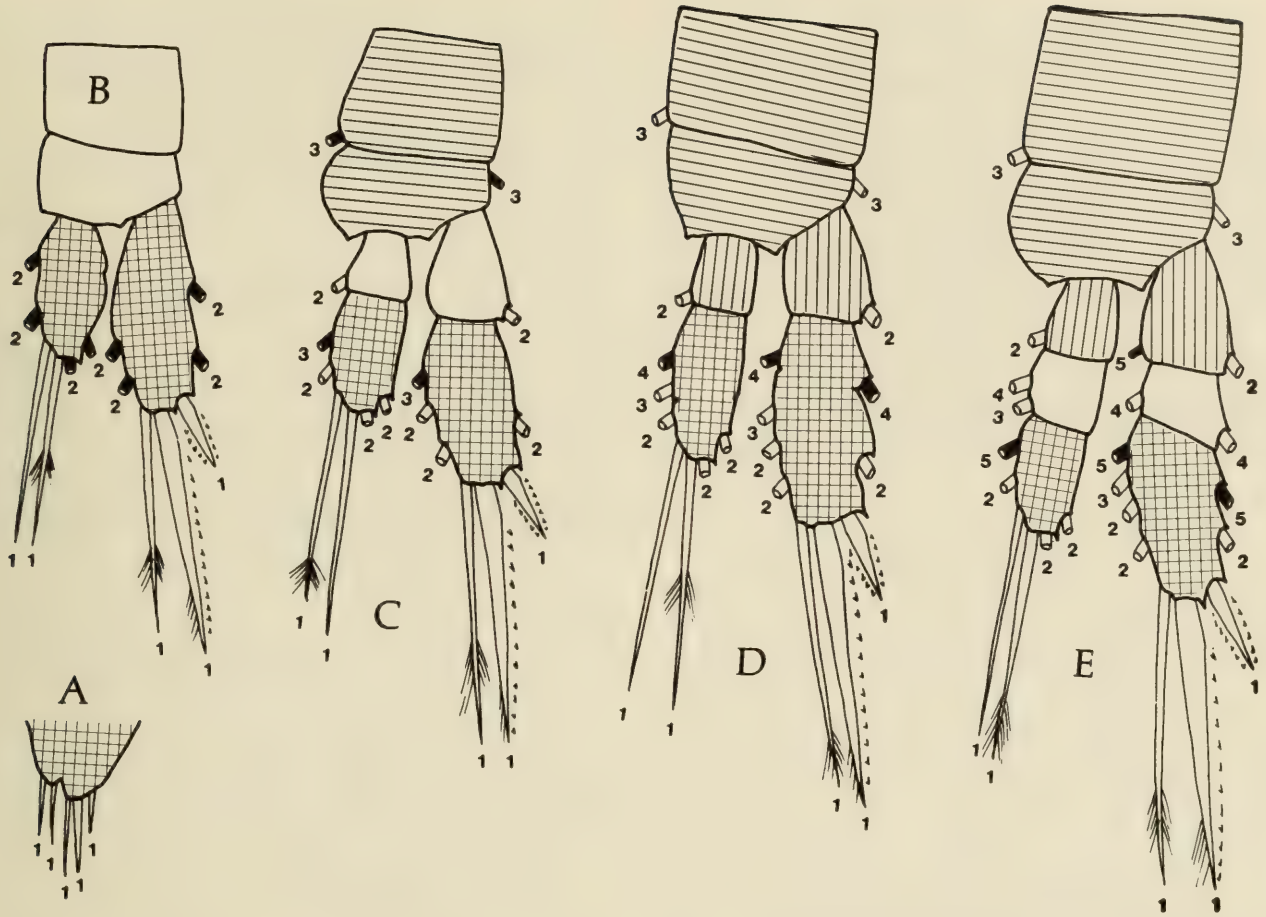

Fig. 13. *Dioithona oculata,* development of leg 3: A, primary bud of copepodid I with 3 setae on outer lobe and 2 setae on inner lobe. B–E, reorganized legs of copepodids II–V respectively. Oldest segment cross-hatched, youngest segment clear, oldest intermediate segment horizontally-hatched, youngest intermediate segment vertically-hatched. Oldest setae from copepodid I (#1's) are long; all others are cropped and new setae are black. New setae added to copepodids II–V are labeled #2–#5 respectively.

proximal to the distal ramal segment. On this new exopodal segment are the older, proximal-most, outer spine and inner seta, and on this new endopodal segment are two older, proximal-most, inner setae of differing ages (Fig. 13E). New setae of CV not formed within a seta of CIV are the small thin inner seta of Re1, the proximal-most inner seta on the distal endopodal segment, and the proximal-most inner seta and outer spine of the distal segment of the exopod.

Thus, for *D. oculata,* new leg segments appear to divide proximally from the distal-most, and oldest, segment of each ramus. Beginning at this distal-most and oldest segment, each more proximal, successive segments are younger than distal neighbors. New armament elements usually are formed at the proximal edge of the distal-most ramal segment. Older elements may be found both proximally and distally to this proximal edge. Changes in genetic regulation of element addition could produce the pattern reported by Von Vaupel Klein (1984) for *Euchirella messinensis.* In *D. oculata* a linear, symmetrical sequence of youngest-to-oldest armament elements may develop if new segments are added, continuously, one molt out of register and later than the newly added armament elements.

The addition of ramal segments described above agrees in general with the pattern described by Hulsemann (1991a) for *Drepanopus forcipatus.* A brief discussion of the pattern of development for segments and armament elements of leg 3 of *D. oculata* appears in Ferrari (1991).

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RENOCILA LORIAE AND *R. RICHARDSONAE* (CRUSTACEA: ISOPODA: CYMOTHOIDAE), EXTERNAL PARASITES OF CORAL REEF FISHES FROM NEW GUINEA AND THE PHILIPPINES

Ernest H. Williams, Jr. and Lucy Bunkley-Williams

Abstract.—*Renocila loriae,* is described from *Apogon* (*Pristiapogon*) sp. collected at Motupore Island, Papua New Guinea; and *R. richardsonae,* is described from *Parupeneus macronema* collected at Jolo Island and a "snapper" collected at Bubuan Island, Philippines. *Renocila loriae* is distinguished by reduced posterolateral projections of the pereonites and long exopods of the uropods with acute apexes; and *R. richardsonae* by the combination of pereopods 1–2 with produced posterodistal corner of basis and pereopods 1–6 with knobs on distal outer margin of ischium. *Renocila richardsonae* is also the largest known species (>33 mm) of this genus. The diagnosis of the genus *Renocila* must be modified to incorporate the reduced projections in pereonites 6–7 of *R. loriae,* and the antenna 2 being longer than 1 in *R. colini.* Lutjanidae or Nemipteridae and Mullidae are new host families for *Renocila,* while the Apogonidae act as host to the most species ($n = 5$) of *Renocila.* A key to the known species of *Renocila* is provided.

Williams & Williams (1980) established a circumtropical distribution for the genus *Renocila* by describing four new species from the Caribbean and the eastern Pacific. Bruce (1987b) further expanded the known range across Australia, and Williams & Williams (1987) extended the range up to the subtropical, northwest Pacific. The present study describes two new species from the western Pacific.

Materials and Methods

Materials and methods largely follow Williams & Williams (1987). Measurements are in mm unless otherwise stated. Some of the fish hosts (USNM 231172–74 and 40949) were collected with dynamite by the U.S. Bureau of Fisheries Albatross Philippine Expedition 1907–1909. A practice that is still destroying coral reefs in the Philippines.

Renocila loriae, new species

Fig. 1

Type material.—Holotype female (USNM 244233), allotype associated male (USNM 250995).

Type host.—*Apogon* (*Pristiapogon*) sp. (Apogonidae) 4.5 cm SL, 6.0 cm TL (USNM 320229).

Type locality.—Coral Sea, Motupore Island, southeast of Port Moresby, Papua New Guinea, 09°41′59″S 147°28′12″E, (Jul 1988).

Attachment position.—Attached on head (P. L. Colin, pers. comm.). Attachment wounds above both eyes on sides of head, larger (female) on right. Isopods were detached from the host when received.

Description, holotype female.—Total length 12.0 (11.3 excluding uropods), maximum width 6.0, with eyed embryos in brood pouch. No remnants of appendix masculina or penes lobes. Body elliptical.

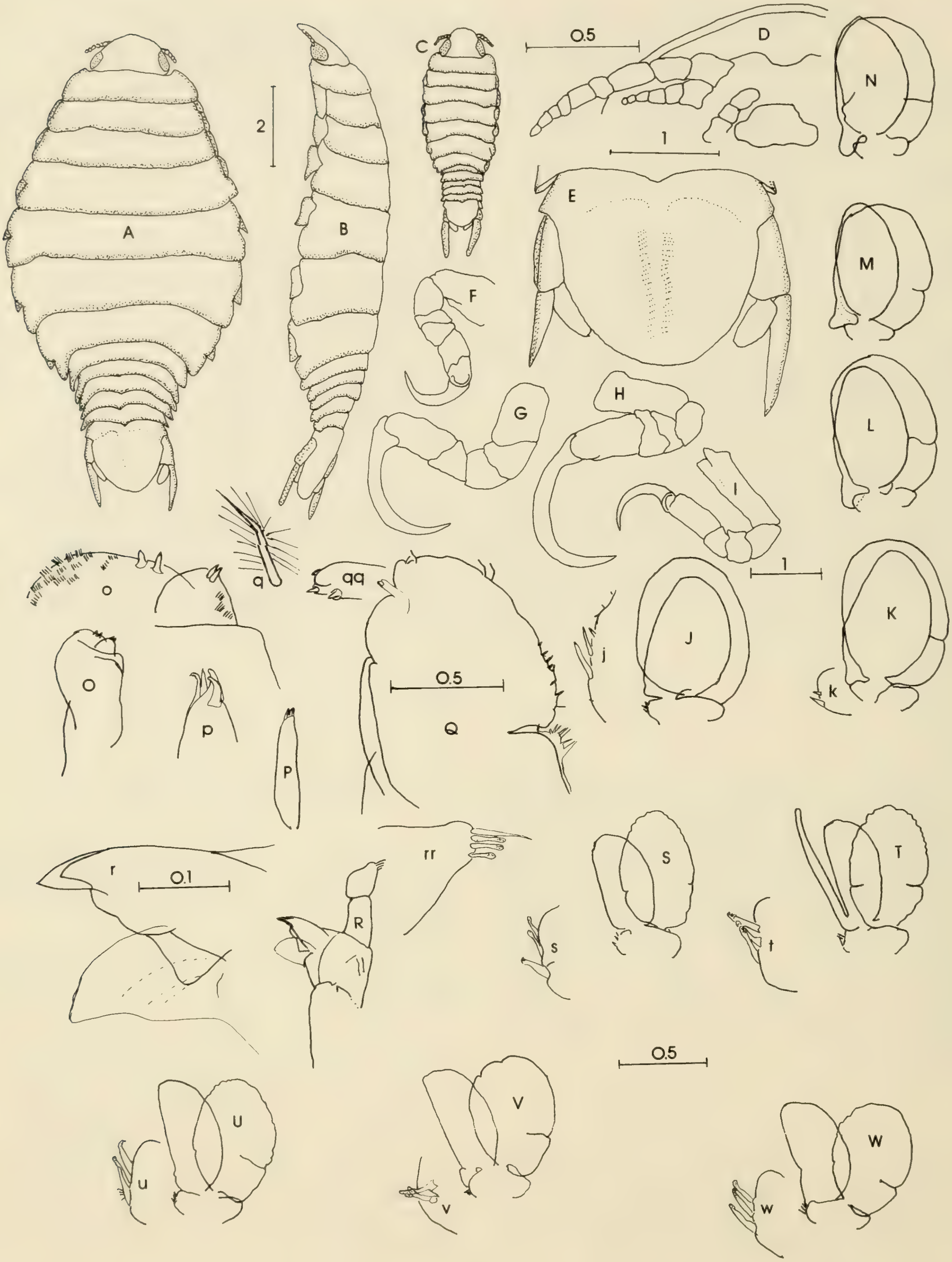

Fig. 1. A–W. *Renocila loriae,* new species (A–B, D–R = female holotype; C, S–W = male allotype) (Scale bars in mm; scale of A–C equal; scale of E–I equal; scale of J–N equal; scale of O–R equal; scale of o–r, qq, rr equal; and scale of S–W equal). A, Dorsal view; B, Lateral view; C, Dorsal view; D, Head, ventral view; E, Pleotelson and uropods, dorsal view; F, Pereopod 1; G, Pereopod 2; H, Pereopod 4; I, Pereopod 7; J, Pleopod 1; j, Seta of base of pleopod 1; K, Pleopod 2; k, Seta of base of pleopod 2; L, Pleopod 3; M, Pleopod 4; N,

Antennae 1, almost twice as long as antennae 2, 9-segmented, not reaching posterior border of head; antennae 2 5-segmented, very short, reaching third article of antennae 1. Anterior margin of head rounded, not flexed ventrally. Coxae of pereonites 4–7 projecting laterally. Posterolateral angle of pereonite 7 slightly produced. Pleonites 3–5 with pointed projection at middle of posterior border of segment. Pleotelson as wide as long. Expopods of uropods extending beyond posterior end of pleotelson, more than twice as long as endopods, apex acute. Pereopods without swelling of dactyls or lobate posterodistal corners of propodus. Dactyls increasing in length from 1 to 4–5 (which are equal) then decreasing to 7. Pleopods lamellar, base of 1–2 with few simple setae. Color, gray with diffuse black pigment spots. Posterior borders of all segments, anterior border of head, and lateral margins of uropods outlined by dark concentration of pigment spots. Pigment spots more diffuse on ventral surface.

Allotype male.—Total length 6.0 (5.0 without uropods), maximum width 2.0. Male similar to female, except smaller and with more narrow body, coloration similar. Appendix masculina approximately ¼ longer than endopod of pleopod 2, almost as long as exopod, darkly pigmented, unlike remainder of pleopod. Base of each pleopod with 3 coupling setae. Penis lobes small, conical processes.

Reproduction.—Eyed embryos (*n* = 3) from brood pouch of female. Typical oval body, rectangular head, eyes black. Total length 1.1, maximum width 0.5.

Habitat and abundance notes.—Shallow coral reef. This isopod is apparently not very common at Motupore Island (P. L. Colin, pers. comm.). We were not able to find any additional specimens during 18 man-hours (11 scuba dives, EHW No. 1426–1436) of diving there 16–18 August 1988, although we examined thousands of cardinalfishes during day and night dives.

Etymology.—The name is in honor of Lori Colin, who helped in collecting this and other isopods from fishes in New Guinea.

Remarks.—The lack of posterolateral projections of pereonites 5–6, and slight projection of 7, of *R. loriae* separate it from all of the known species of *Renocila* and from Bruce's (1987b) definition of the genus. This character is important because it was one of the useful distinctions between the genera *Renocila* and *Anilocra*. Pereonites 6–7 of *R. loriae* are more similar to those found in species of *Anilocra*, than those of *Renocila*; however, this species otherwise conforms to the genus *Renocila*. The uropods of this species are similar to those of *R. heterozota* Bowman & Mariscal and *R. yamazatoi* Williams & Williams, except that the apex of the exopods is acute. The dark pigment stripes on the body and midposterior projections of the pleonites are similar to, but less intense than, those found in *R. bollandi* Williams & Williams.

Renocila richardsonae, new species

Figs. 2–4

Renocila ovata: Richardson, 1910:22
Renocila sp. Bruce, 1987:169

Specimens examined.—Six specimens: 1 male and 1 female, 18 Sep 1909, Sulada Id. Dyn., U.S. Bureau of Fisheries Albatross Philippine Expedition 1907–1909 (USBFAPE), USNM 231173; USBFAPE 9095550B, N. Sulada Island, dynamite, 14

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Pleopod 5; O, Maxilla 2; o, Distal lobes of maxilla 2 with semilunar pectinate scales; P, Maxilla 1; p, Apex of maxilla 1; Q, Maxilliped; q, Seta from margin of maxilliped; qq, Apex of maxillipedal palp; R, Mandible & palp; r, Incisor process of mandible; rr, Apex of mandibular palp; S, Pleopod 1; s, Coupling seta of base of pleopod 1; T, Pleopod 2; t, Coupling seta of pleopod 2; U, Pleopod 3; u, Coupling seta of pleopod 3; V, Pleopod 4; v, Coupling seta of pleopod 4; W, Pleopod 5; w, Coupling seta of pleopod 5.

shots, 10–15 feet, 17 Sep 1909(?). 1 male and 1 female, 7 Mar 1908, Jolo Island, Philippines, *Pseudupeneus macronema,* 7 and 3/16 inches long, "In each the smaller isopod was on caudal peduncle and the larger on side of fin under soft dorsal.", USNM 231174; USBFAPE 9085174F, Jolo W of anchorage, dynamite, 4–10 feet; 5°58′N, 121°06′E. 1 male, 14 Feb 1908, Bubuan Island, southwest side of Island, off Jolo, Jolo Island, Philippines, Sulu Archipelago, Sulu Sea, "On tail of snapper," 06°03′07″N, 122°14′13″E, USNM 40949; USBFAPE 9085140B, vicinity of Jolo, dynamite, 8–20 feet; 6°11′N, 120°58′E. 1 female, 21 Sep 1909, Singaan Id. Dyn., USNM 231172; EUSBFAPE 9095562E, N Singaan Island between Jolo and Tawi Tawi, dynamite, 17 shots, 9–25 feet; 5°45′N 120°25′E.

Type specimens.—Holotype (female) USNM 231173, allotype (associated male) USNM 250607 (formerly USNM 231173); 4 paratypes USNM 40949, 231172, 231174.

Type locality.—Sulada Island, Philippines 05°50′N 120°47′E.

Host.—"*Pseudupeneus macronema*" was indicated as the host for specimens USNM 231174. This is probably the longbarbed goatfish, *Parupeneus macronema* (Lacepede) (Mullidae). Unfortunately, Fischer & Whitehead (1974) suggest that this fish does not occur in the Philippines. "Snapper" (Lutjanidae? Nemipteridae?) was noted as the host for specimen USNM 40949. All fishes deposited in the USNM Ichthyology Collection with similar localities and dates of USNM 40949 lacked damage indicating the attachment of an isopod.

Attachment position.—The USNM 231174 label records the male attached on the caudal peduncle of the host and the female forward of the male on the side of the host under the soft dorsal fin. The record also suggests that this was seen more than once, although only one pair of isopods was preserved. The USNM 40949 (Fowler 1931) record was from the tail of snapper. We did not observe these hosts. No damage to the host, which could have served to substantiate the record, was noted on the labels or by Richardson (1910).

Description, holotype female.—Total length 35.2, maximum width 16.1. No remnants of appendix masculina or penes lobes present. Body rectangular. Antennae 1 7–8-segmented (7 segments in females with fully developed brood pouches, the proximal segment appears as if two segments have fused to make one large segment), reaching midlength of pereonite 1 sometimes a little farther but never reaching posterior margin of pereonite; first 2 segments of antennae 1 broadened and flattened. Antennae 2 7–8-segmented, approximately ⅔ length of antennae 1; much thinner than antennae 1. Anterior margin of head straight. Coxae of pereonite 7 covered laterally by posterolateral projections of pereonite 6. Posterolateral angles of pereonites 6–7 produced, 7 covering lateral margins of pleonites 1–3 and extending posterior to anterior margin of pleotelson. Pleotelson wider than long. Uropods not extending to posterior end of pleotelson, exopod longer than endopod. Pereopods without swellings of dactyls or lobate posterodistal corners of propodus. Pereopods 1–2 (and 3 in one specimen) with projection of posterodistal corner of basis. Pereopods 1–6 with knobs on distal outer margin of ischium. Pereopods very gradually increasing in length from 1 to 6, 7 abruptly longer. No spines or setae present on any pereopods. Proximomedial lobe of endopods 3–5 of pleopods becoming progressively larger. Pleopods 3–4 with small folds on endopod, more pronounced on endopod of 5. No coupling setae on bases of pleopods. Color (in alcohol) uniform beige.

Allotype male.—Total length 18.0, maximum width 7.5. Similar to female, except smaller and with more narrow body shape, coloration similar. Projections on basis and ischium of pereopods lacking in the smaller two specimens. In the largest male, however, projections of the distal outer margin of the basis of pereopods 1 and 2 are apparent, no swellings or projections on the ischium of the pereopods are noticeable. Pleopods lamellar, bases of 1–2 with coupling setae. Appendix masculina approximately ⅔ as long as endopod of pleopod 2. Penis lobes small, conical process.

Other females.—$n = 2$. Total length 31.9 & 33.4, maximum width 14.7 & 15.2. No remnants of appendix masculina or penes lobes present.

Other males.—$n = 2$. Total length 14.6 & 18.0, maximum width 5.6 & 7.5. Similar to allotype.

Reproduction.—Uneyed embryos from brood pouch of female (USNM 231172), not counted, as number remaining may be less than those originally present. Typical oval body, rectangular head. Total length 1.89–2.26 (1.99), maximum width 1.06–1.28 (1.11) ($n = 10$).

Habitat, relationship and association notes.—Collected between 1.3 and 8.3 m depth apparently in coral reef areas. Pereopods, pleopods and portions of pereonite 7 were bitten off or damaged presumably by other fishes. Hydroids (Coelenterata: Hydroidea) and other encrusting organisms covered portions of the pleotelson, pleopods and pereonite 7.

Etymology.—The specific name is in honor of Harriet Richardson and her work with isopods.

Remarks.—*Renocila richardsonae* differs from all known species of *Renocila* by having pereopods 1–2 with projections on posterodistal corner of basis, pereopods 1–6 with knobs on distal outer margin of ischium, and by its large size.

The oostegites of pereonites 1–4 were fully formed in the female USNM 231174, while there were no oostegites on pereonites 5–7. This suggests that this female was in the process of molting when preserved, and that oostegites in this species form in a single molt.

The confirmed hosts for species of *Renocila* have been small coral reef fishes (Bruce 1987b). *Renocila bollandi* has been reported from scorpaenids, which are moderately-sized fishes, but has thus far only been collected from immature hosts (Williams & Williams 1987; unpubl. data). The 18.3 cm goatfish is a departure from this pattern.

Richardson (1910) assumed that the specimen she examined (USNM 40949) (Fig. 3A, B) was a male, possibly because the appendix masculina is approximately ⅔ the length of the endopod of pleopod 2. The specimen may be a male-female transitional since the pereopod projections of the female are beginning to develop in this specimen, and it seems to be intermediate in body shape between the three females (including Fig. 2A, B) and the two males (Fig. 2C, D). Actually, the sexual status of this specimen cannot be determined without a series of specimens to study and/or histological examination of the reproductive organs.

Discussion

The genus *Renocila* is characterized by having antenna 1 longer and broader than antenna 2 (Bruce 1987b) and the posterolateral margins of pereonites 6–7 produced (Bowman & Mariscal 1968, Bruce 1987b). Antenna 2 of *R. colini* Williams & Williams is longer and only slightly narrower than antenna 1 (Williams & Williams 1980); and the posterolateral margins of the pereonites of *R. loriae* are not produced (slightly in pereonite 7). These two species are otherwise in agreement with the genus, and they should remain in *Renocila*. These characters should be modified in the diagnosis of the genus.

Size should never be used as a diagnostic character, but size alone once conveniently distinguished members of the genera *Renocila* and *Anilocra*. Our description of *A. partiti* (Williams & Williams 1981, 12–16 mm) and the description of *A. apogonae* (Bruce 1987a, 11.5–19.5 mm) and *A. pomecentri* (Bruce 1987a, 11.0–12.5 mm) defined species of *Anilocra* that were as small

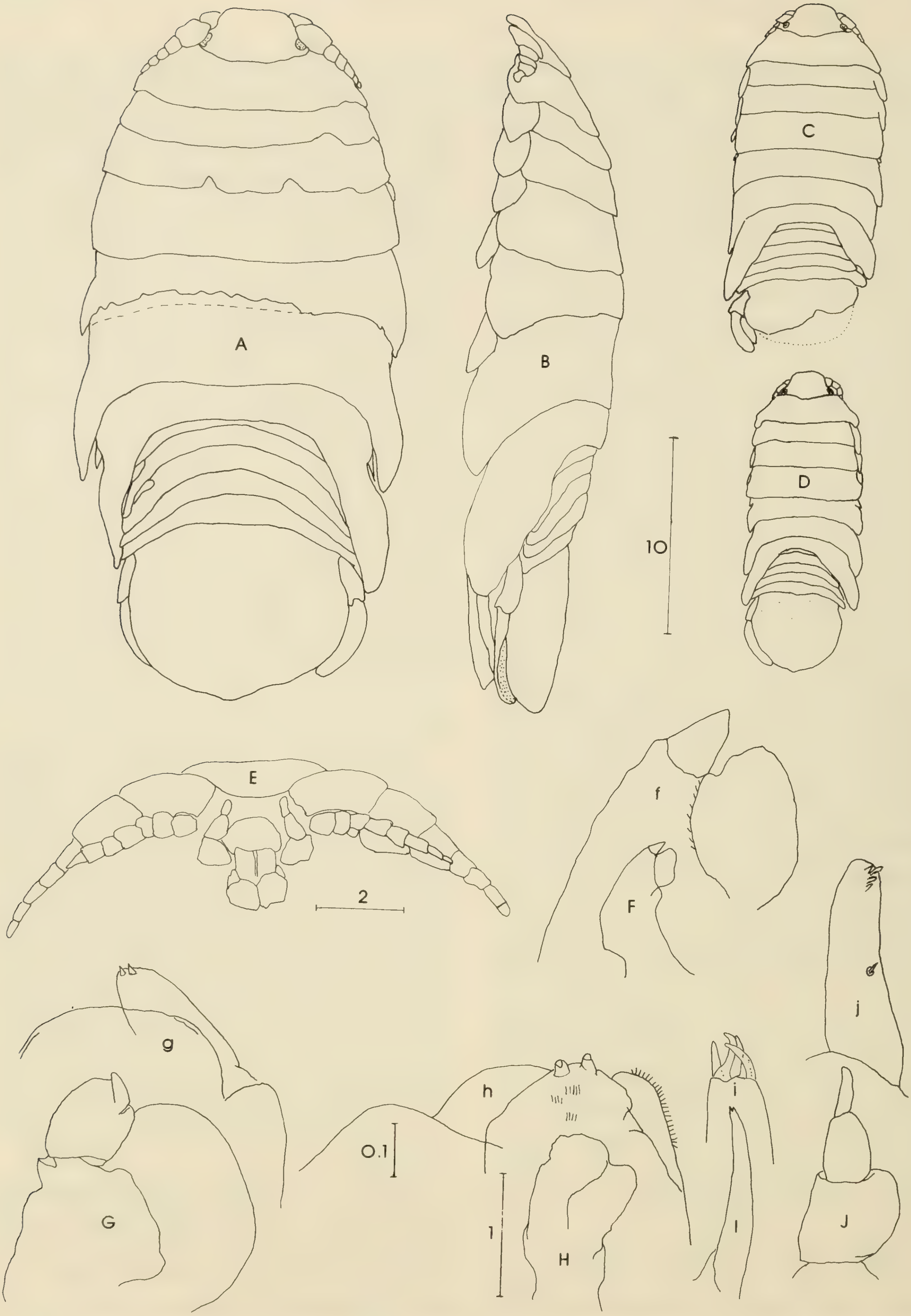

Fig. 2. A–J. *Renocila richardsonae,* new species (Scale bars in mm; scale of A–D equal; scale of f–j equal; and scale of F–J equal) (A–B, E, holotype; C, allotype; D, male paratype USNM 231174; F–J, Female paratype USNM 231174). A, Dorsal view; B, Lateral view; C, Dorsal view; D, Dorsal view; E, head, ventral view; F, Mandible; f, Incisor process of mandible; G, Maxilliped; g, Apex of maxillipedal palp; H, Maxilla 2; h, Distal lobes of maxilla 2 with semilunar pectinate scales; I, Maxilla 1; i, Apex of maxilla 1; J, Mandibular palp; j, Apex of mandibular palp.

as many species in the genus *Renocila. Renocila richardsonae* (32–35 mm) is the largest member of this genus ever described. It is more similar in size to members of the genus *Anilocra* than other members of its genus. Members of the genus *Renocila* could once colloquially be categorized as small isopods on small fishes, and *Anilocra* as large isopods on large to moderate-sized fishes; now exceptions exist.

The Apogonidae commonly act as hosts for members of this genus. *Renocila colini* occurs on Caribbean, *R. thresherorum* Williams & Williams on eastern Pacific, *R. plesiopi* Bruce on Australian, *R. loriae* on Papua New Guinean, and *R. ovata* Miers on Indonesian cardinalfishes (Williams & Williams 1980, Bruce 1987a). The change in species of *Renocila* on cardinalfishes at either end of the Great Barrier Reef, while the *Anilocra* on the same hosts remained the same, supports the restricted geographic range of many species of *Renocila* discussed by Williams & Williams (1987). Bruce (1987a) suggests that *R. ovata* has a wide geographic distribution. More field work is necessary to resolve host specificity and geographic ranges of most species in this genus.

Since our key (Williams & Williams 1987) to the known species of *Renocila,* six species have been added, two new combinations created, and one species eliminated (Bruce 1987b, 1991, & present paper). Bruce & Harrison-Nelson (1988) also pointed out shortcomings in our 1987 key. Therefore, a new key is provided.

Key to the Species of *Renocila* Based on Female Specimens (Females are not known for *R. limbata, R. periophthalma,* and *R. recta*):

1a. Exopod of uropod approximately twice as long as endopod 2

1b. Exopod of uropod much less than twice as long 5

2a. Posterolateral projections on pereonites 6–7
Parasites of damselfishes 3

2b. Pereonites 6–7 not projected
Parasites of cardinalfishes or scorpionfishes 4

3a. Posterolateral projection of pereonite 7 extends to pleonite 2
Posterolateral projection on pereonite 4 .... *R. yamazatoi*

3b. Posterolateral projection of pereonite 7 extends to pleotelson
Pereonite 4 without posterolateral projection ....*R. heterozota*

4a. Exopod of uropod much more than twice as long as endopod
Uropod rami posteriorly acute
Pleonites with acute dorsomedial processes ....*R. loriae*

4b. Exopod of uropod less than twice as long as endopod
Uropod rami posteriorly blunt
Pleonites lack acute dorsomedial processes ....*R. curtipinna*

5a. Posterolateral projection on pereonite 4 6

5b. Pereonite 4 without posterolateral projection 9

6a. No nodules on dactyls of pereopods
No carinate process on posterodistal margin of pereopods
Posterolateral projection of pereonite 4 prominent 6

6b. Nodules on dactyls of pereopods 1–3 or 4
Carinate process on posterodistal margin of pereopods 1–3
Posterolateral projection of pereonite 4 moderate 7

7a. Midposterior projections of all segments
Pleon broad
Antennae 2 with 3 articles ....
.......................*R. bollandi*

7b. No midposterior projections of segments
Pleon narrow, tapering posteriorly
Antennae 2 with 9 articles ....
.... *R. plesiopi*

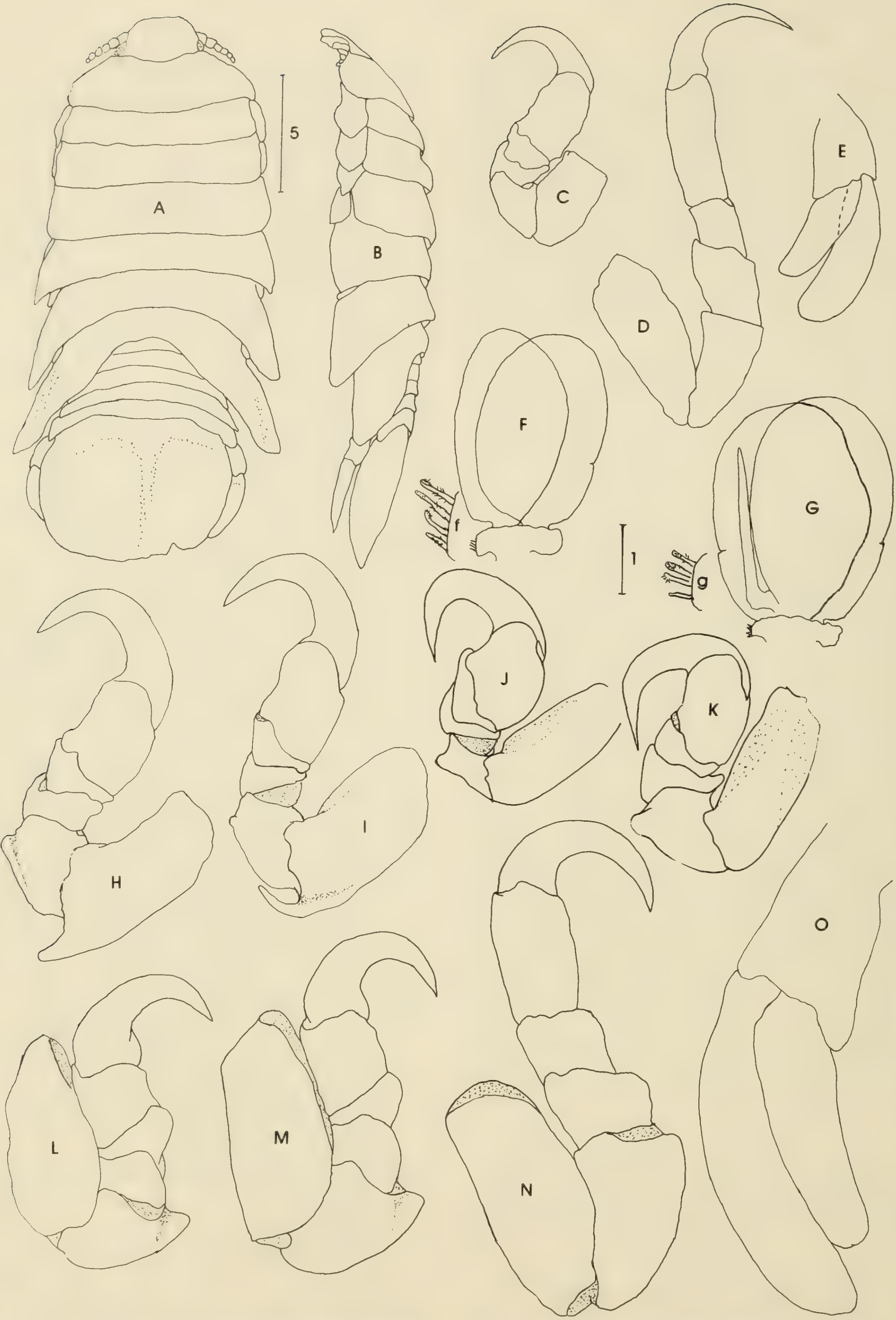

Fig. 3. A–O. *Renocila richardsonae,* new species (Scale bars in mm; scale of A–B equal; and scale of C–O equal) (A–B, male or male-female transitional paratype USNM 40949; C–G, male paratype USNM 231174; H–O, holotype). A, Dorsal view; B, Lateral view; C, Pereopod 1; D, Pereopod 7; E, Uropod; F, Pleopod 1; f, Coupling seta of base of pleopod 1; G, Pleopod 2; g, Coupling seta of base of pleopod 2; H, Pereopod 1; I, Pereopod 2; J, Pereopod 3; K, Pereopod 4; L, Pereopod 5; M, Pereopod 6; N, Pereopod 7; O, Uropod.

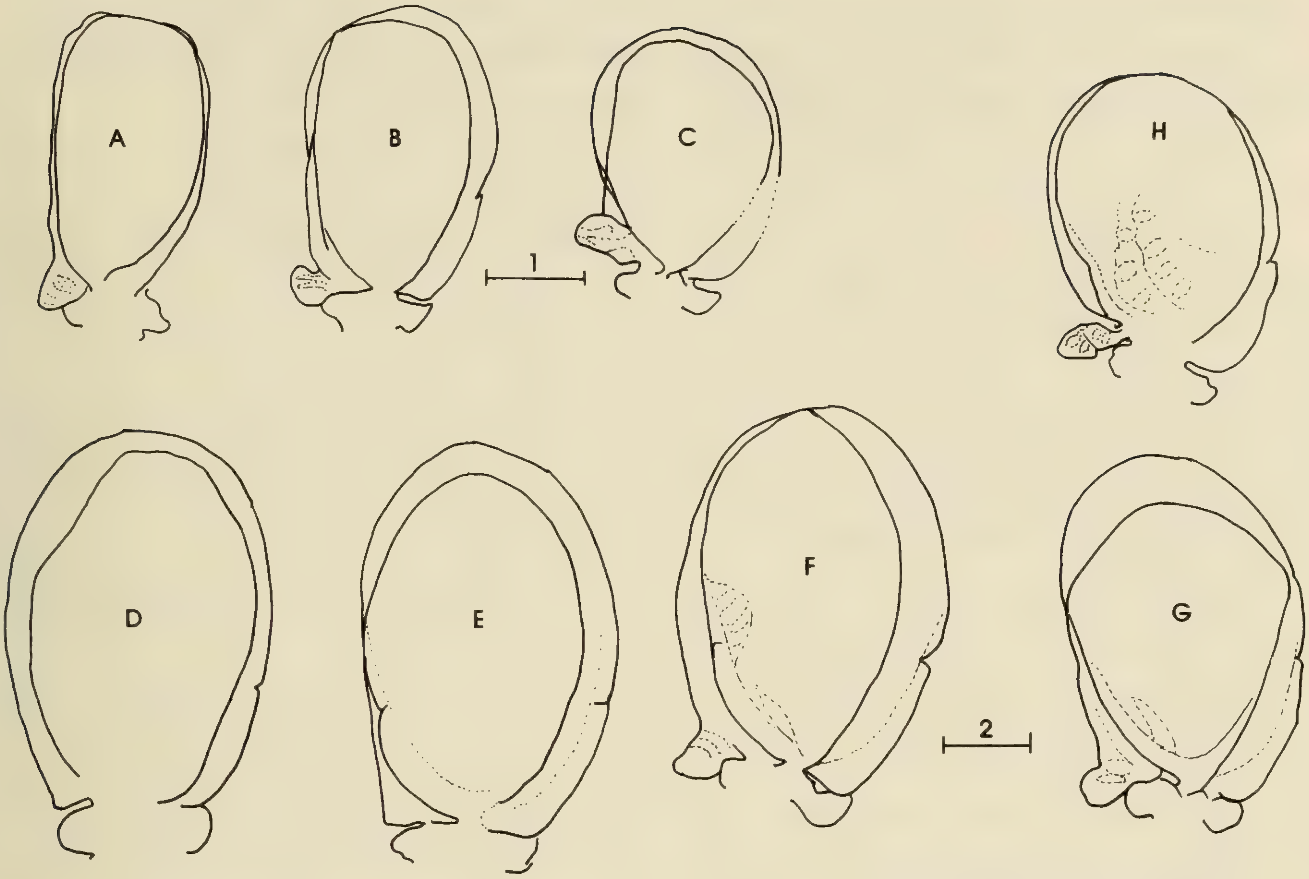

Fig. 4. A–G. *Renocila richardsonae,* new species (Scale bars in mm; scale of A–C equal; and scale of D–H equal) (A–C male paratype USNM 231174; D–H female paratype USNM 231174). A, pleopod 3; B, Pleopod 4; C, Pleopod 5; D, Pleopod 1; E, Pleopod 2; F, Pleopod 3; G, Pleopod 4; H, Pleopod 5.

8a. Uropods do not extend to end of pleotelson
Posterolateral projections rounded
Nodules on pereopods 1–3 . *R. ovata*

8b. Uropods almost always extend beyond end of pleotelson
Posterolateral projections acutely pointed
Nodules on pereopods 1–4 .... *R. kohnoi*

9a. Carinate process on posterodistal margin of pereopods 1–3
Nodules on dactyls of pereopods 1–3 10

9b. No carinate process on pereopods
No nodules on dactyls of pereopods 11

10a. Dactyls as long as propodus
Antennae 1–2 approximately equal in length
Anterior margin of head rounded
.... *R. alkoo*

10b. Dactyls longer than propodus
Antennae 1 much longer than 2
Anterior margin of cephalon truncated .... *R. indica*

11a. Pereonite 7 posterolateral projection to pleonite 5 or pleotelson
Anterior of cephalon straight
Antennae 1 much longer than 2
.... 12

11b. Pereonite 7 posterodistal projection reaches pleonite 1–3
Anterior of cephalon rounded
Antennae 1–2 similar in length 14

12a. No rostral point
Pleotelson wider than pleon
No carina on ischium of pereopods .... *R. richardsonae*

12b. Triangular rostral point between bases of antenna 1
Pleon wider than pleotelson

Prominent curved carina on pereopods 1–3 ischium . . *R. quadrata*

13a. Coxae of pereonite 7 projects laterally
Coxae of pereonites 6–7 acutely pointed
Body robust . . . . . . *R. thresherorum*

13b. Coxae not projecting laterally
Coxae of pereonites 6–7 bluntly rounded
Body elongate oval 12

14a. Posterolateral projection of pereonite 7 reaching pleonite 1
Posterolateral angle of pereonite 5 produced
Antennae 2 longer than 1 . . *R. colini*

14b. Posterolateral projection of 7 reaching pleonite 2 or beyond
Posterolateral angle of pereonite 5 not produced
Antennae 1 longer than or equal to 2 15

15a. Lateral margin of pereonites 4–7 notched
Posterolateral projection of pereonite 6 covers coxae of 7
Black . . . . *R. bowmani*

15b. Lateral margin of pereonites 4–5 not notched
Posterolateral projection of 6 does not cover coxae of 7
Brown . . . . *R. Waldneri*

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GUITONIA TROGLOPHILA, A NEW GENUS AND SPECIES OF ANCHIALINE CRAB FROM THE GALÁPAGOS, ISLA SANTA CRUZ, GRIETA DE CALETA LA TORTA (CRUSTACEA: DECAPODA: BRACHYURA)

John S. Garth and Thomas M. Iliffe

Abstract.—The genus *Guitonia* Garth, new genus, is established to accommodate *Guitonia troglophila* Garth & Iliffe, new species, described herein. Collected with a baited trap in Grieta de Caleta la Torta, Isla Santa Cruz, this crab is the second anchialine species to be collected in the Galápagos Islands, the first being *Garthiope anchialina* Guinot & Iliffe, 1991, from Cueva de la Cadena, Isla Isabela (Albemarle). Unlike the first species, *Guitonia troglophila* is from a cave having no direct communication with the open sea. It shows incipient modifications toward a troglobic existence, including reduced eyestalks, attenuated appendages, and sensory setae on its carapace and legs.

In 1987, an expedition of two months' duration to the Galápagos Islands permitted the junior author to explore the marine caves, both submarine and anchialine, of several islands of that archipelago, and to bring back a very interesting collection of troglobitic and troglophilic organisms (cf. Iliffe 1991). Two species of crabs were thus collected, both of them new. The one, found in Cueva de la Cadena, Isla Isabela (Albemarle), belongs to the recently established genus *Garthiope* Guinot, 1990; the other, which came from a cave situated in a tectonic fissure in Grieta de Caleta la Torta, Isla Santa Cruz, requires the establishment of a new genus. Of apparent xanthid affinities, the new genus must be considered incertae sedis pending confirmation by the male first pleopod; the unique holotype is female.

Guitonia Garth, new genus

Carapace transversely oval, width ca. 1.46 times length. Regions well marked and granulate anteriorly, smooth and bare posteriorly. Front 0.28 times width, scarcely advanced beyond level of anterolateral marginal arc, lobes separated by a recessed pit, as seen in frontal view; a similar pit separating front from orbital margins. Basal antennal article not reaching front; antennules folding transversely. Orbits failing to close externally at level of postorbital (first anterolateral) tooth, instead communicating by means of shallow trough or gutter with second anterolateral tooth. Teeth 2–5 arcuate, marginally denticulate, incurving, third tooth longest.

Chelipeds unequal, major manus high, with broad digital tooth; minor manus elongate, fingers slender, deflexed.

Walking legs attenuated, margins spinulous and hairy, dactyls straight.

Female abdomen with seven segments; male unknown.

Type species.—By original designation, *G. troglophila* Garth & Iliffe.

Etymology.—The genus is named for the distinguished carcinologist, Danièle Guinot, in the form of an anagram, in which the first three letters of the name read forward, the last three, backward.

Remarks.—Because of the provenience of this unusual small crab, an anchialine cave in the Galápagos Islands, troglomorphic adaptations, such as absence of color, absence of corneal pigmentation, reduction of eye size, attenuation of appendages, and provision of sensory setae to compensate for lack of vision, were anticipated. Although slightly pinkish or orangish when received (from memory, as no color notes were taken), the crab is now uniformly grayish white. Eyes and eyestalks are reduced in size, but have the corneas black-pigmented. The minor cheliped and walking legs are slender and attenuated. The many sensory hairs, or setae, are found on the carapace and minor cheliped, but mainly on the walking legs, where they may serve as food-locating mechanisms in the still, lightless waters of the cave. Those on the mouthparts (maxillipeds) may perform sensory functions consistent with their length and delicacy.

The cave from which *Guitonia troglophila* was collected was inhabited by a number of other troglobitic crustaceans, including ostracods, amphipods, and an atyid shrimp, whose nearest relatives are to be found in caves in the western Atlantic, particularly in the Gulf of Mexico and Caribbean Sea. It was postulated by Kornicker & Iliffe (1989) that their ancestors reached the Pacific before the closure of the Panama land bridge in [mid-] Pliocene. In the case of the ostracod *Danielopolina* and six other invertebrate genera having an amphi-American distribution, their colonization of caves may have begun as early as the Mesozoic, with dispersal through sea-floor spreading (by movement of Tectonic plates). Their fossil record also suggests a Tethyan origin. The closest relatives of *Guitonia troglophila* should, therefore, be sought in anchialine caves of Bermuda, the Bahamas, Puerto Rico, or even the Canary Islands and Ascension Island.

Guitonia troglophila Garth & Iliffe, new species

Figs. 1, 2

Type.—Female holotype, AHF No. 871, from Grieta de Caleta la Torta (anchialine cave), Isla Santa Cruz, Islas Galápagos, 8 June 1987, Station 87-018, Thomas M. Iliffe, collector.

Measurements.—Female holotype, length of carapace 9.7 mm, width of carapace 14.2 mm, width of front 4.0 mm, length of major chela 9.9 mm, of major dactyl 4.8 mm, height of palm 5.1 mm.

Description.—Carapace (Fig. 1A) broader than long, transversely oval, regions well demarcated anteriorly, elevations sharply granulate, sparsely hairy, intervening depressions smooth or finely granulate, as is posterior ⅖ of carapace. Front slightly advanced over arc of anterolateral margins, bilobate, lobes straight or, in frontal view (Fib. 1B), sinuous, advancing toward broad median V, edge granulate, a recessed pit, similar to median hiatus as seen from below, separating front from orbital margin. Basal antennal article not touching front; antennules folding transversely. Orbits (Fig. 1C) granulate, postorbital tooth lacking; instead, a postorbital notch communicating with a postorbital depression bounded by a granular ridge above and below, the lower ridge representing the forward continuation of the anterolateral margin, and bearing only a suggestion of the normal first anterolateral tooth. Anterolateral margins arcuate, dentate, teeth sharply granulate; of the five teeth (DENTS) of Dana (1852), only four may be seen, the first tooth (D) obsolescent. Second tooth (E) smallest, located the width of the orbit behind the eye; third tooth (N) largest, its external margin longest of any; fourth tooth (T) similar, but only half as long; fifth tooth (S) small; teeth N, T, S spine-tipped and spinulous-margined, teeth from S to E curving successively forward and inward, imparting a broad arc to entire margin. Carapace convex in both directions, gastric region well defined, hepatic and branchial regions swollen and granulate.

Ischium of external maxilliped (Fig. 1E) longitudinally grooved, merus subquadrate, anterior margin sinuous, slightly produced at anteroexternal angle and recessed at anterointernal angle to receive palpus, surface uneven, granulate.

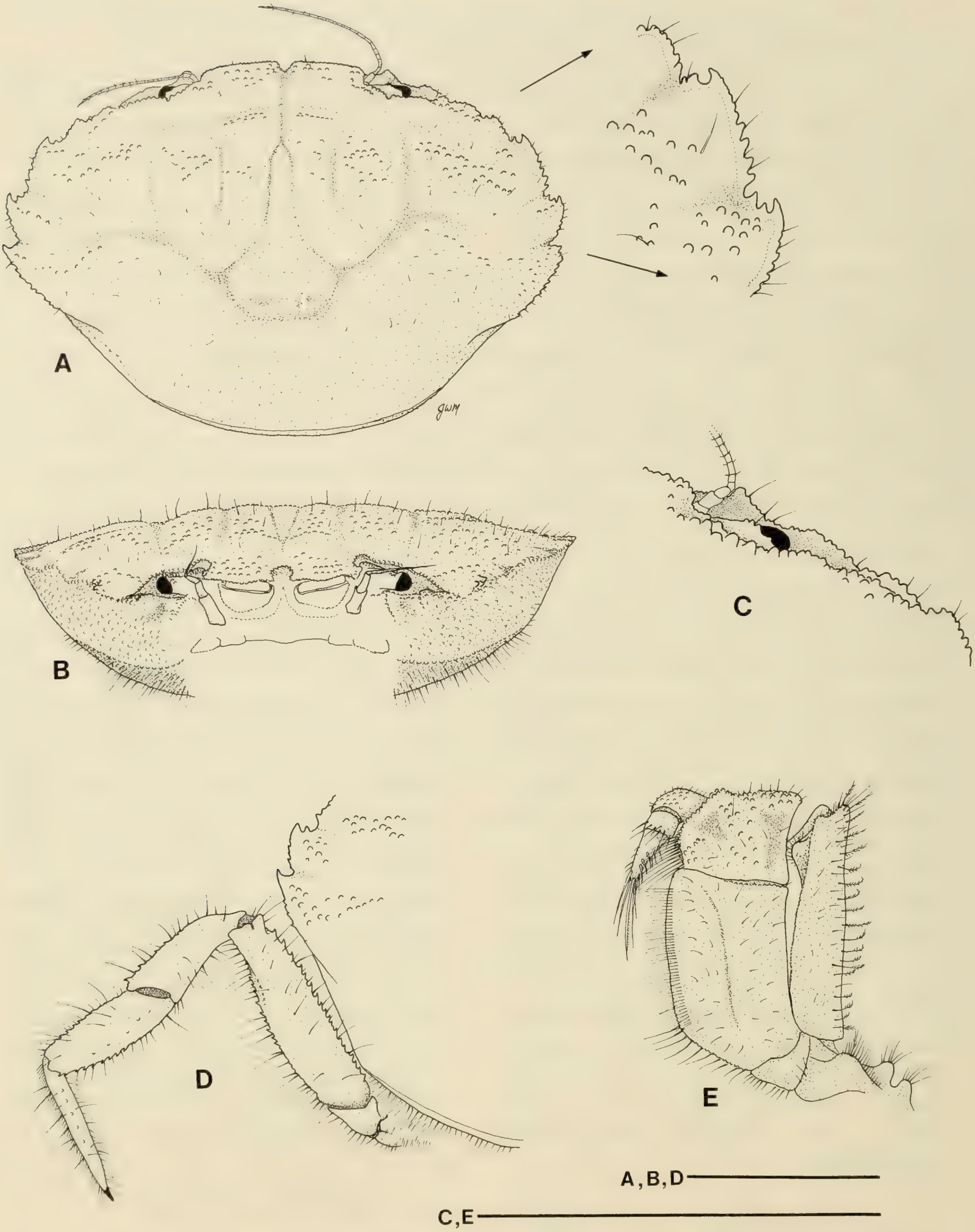

Fig. 1. *Guitonia troglophila,* new species, female holotype, AHF. A, dorsal view of carapace, with detail of anterolateral teeth (E, N, T); B, frontal view of carapace, showing interorbital region; C, dorsal view of right orbital region; D, left fourth walking leg and anterolateral teeth (T, S); E, left outer maxilliped, external view. Scale bar = 5.0 mm. (Drawings by Joel W. Martin.)

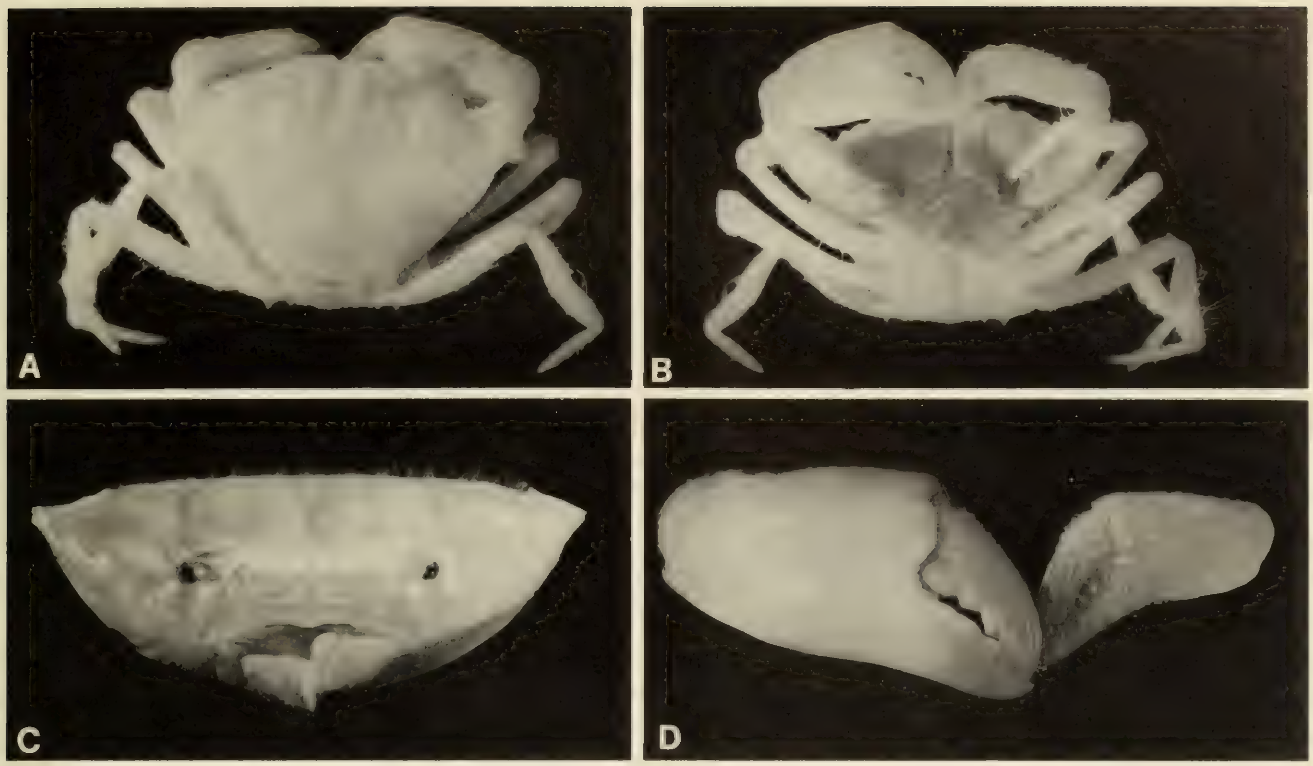

Fig. 2. *Guitonia troglophila*, new species, female holotype, AHF. A, dorsal view; B, ventral view; C, frontal view of carapace; D, outer view of chelipeds. (Photographs by Los Angeles County Natural History Museum.)

Chelipeds (Fig. 2D) unequal, right larger. Major cheliped robust, merus trigonal, margins sharply granulate; carpus granulate, a spine-tipped triangular projection at inner angle; manus granular and hairy, inner superior margin with hooked spinules proximally, upper margin with a granular ridge, lower half of palm smooth and bare, color of propodal finger confined to tip; dactylus with a strong basal tooth, followed by two triangular teeth that interdigitate with two similar propodal teeth. Minor cheliped slender, hairy, spinulate above, fingers strongly deflexed, tips crossing.

Walking legs long, slender, spinuous margined, and hairy, spines often alternately large and small; carpus and propodus of fifth pereiopod (Fig. 1D) together equalling length of merus; dactylus long, straight, but not recurved (as in Goneplacidae), corneous tips amber, incurving.

Abdomen of female with 7 free segments.

Remarks.—*Guitonia troglophila* resembles species of *Micropanope* and a number of other genera with small species as reviewed by Guinot (1967), some of which are panopeine and some xanthine. The troglophilic crab in question cannot readily be placed in any of these genera, yet appears to belong to the ancient fauna of which they are a part. It is therefore placed in a new genus, *Guitonia* Garth, although the female specimen on which it is based does not permit its placement with the certainty that will eventually be possible with the finding of a male and the use of the character of the first pleopod. The uniqueness of the specimen and its unusual provenience appear to justify this course.

Habitat.—Grieta de Caleta la Torta (Fig. 3) is a tectonic fissure located 100 m inland and running parallel to the south coast of Isla Santa Cruz. It is part of a network of similar fissures presumably formed by the slumping along the margins of this volcanic island. A series of deep, clear anchialine pools floored with large collapse boulders are situated at the base of the 20 m deep, 5

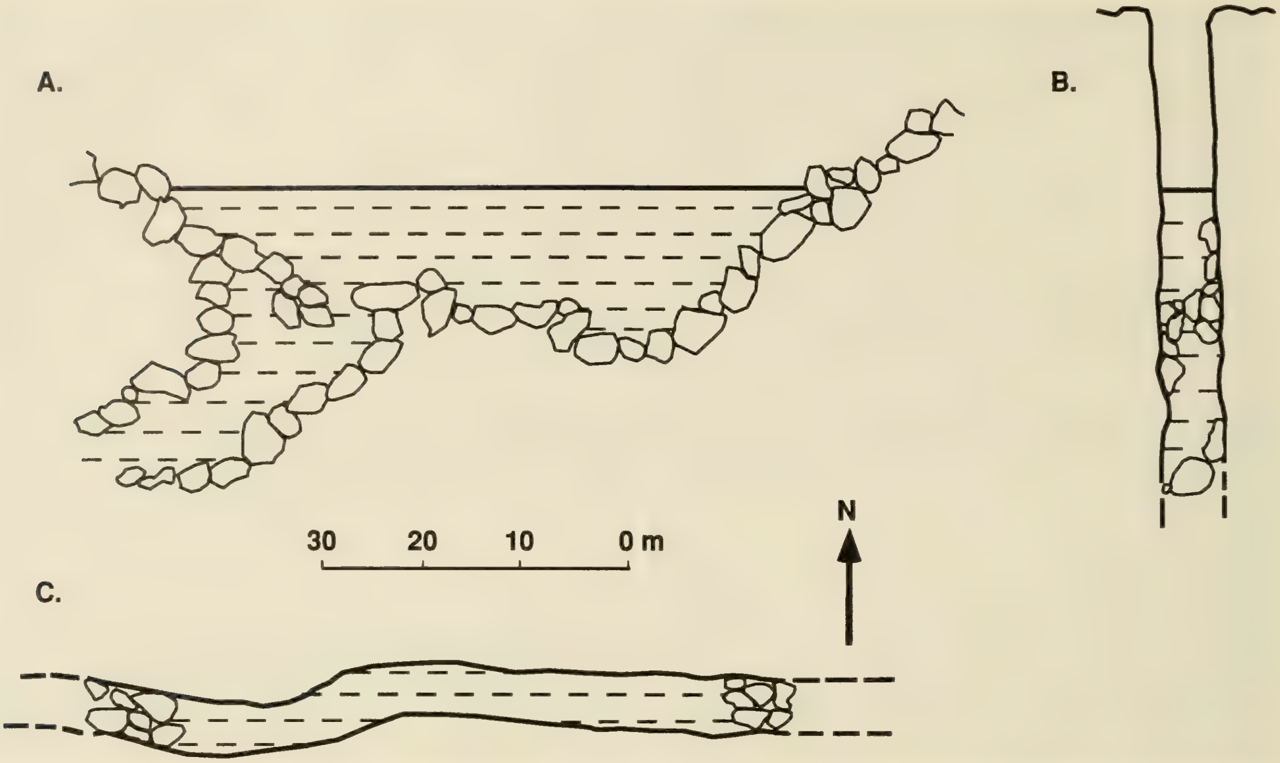

Fig. 3. Profile (A), section (B), and plan (C) maps of Grieta de Caleta la Torta, Isla Santa Cruz, Islas Galápagos. (Drawn by Thomas M. Iliffe.)

m wide fissure. Sections of the pools extend into areas of total darkness beneath wedged breakdown blocks. Salinities at 0, 3 and 17 m depths were 9, 11 and 29 p.p.t., respectively. A single specimen of *Guitonia troglophila* was collected with a plastic bottle trap baited with a crushed crab left overnight at 10 m depth.

Other crustaceans collected from this cave include troglobites showing affinities to deep sea or Caribbean and West Atlantic species (Iliffe 1991). The shrimp *Typhlatya galapagensis* Monod & Cals, 1970, belongs to an exclusively troglobitic genus comprising nine species with distribution including the Galápagos, West Indies, Mexico (Yucatan and Campeche), Ascension Island, and Bermuda. The halocyprid ostracod *Danielopolina styx* Kornicker & Iliffe, 1989, is a member of a genus with both anchialine species on the Yucatan Peninsula, Cuba, the Bahamas and Canary Islands and a deep-sea species in the equatorial Atlantic. The cypridinid ostracod *Skogsbergia galapagensis* Kornicker & Iliffe, 1989, is most closely related to a congener, *S. lerneri* (Kornicker, 1958), an open water species distributed in the Gulf of Mexico and Caribbean Sea. Three species of blind troglobitic amphipods collected from this pool each represent a different family. *Galapsiellus leleuporum* (Monod, 1970) from the family Melitidae is present in other anchialine pools on both Islas Santa Cruz and Isabela. It is apparently derived from the widespread marine genus *Eriopisa* (Barnard, 1976). Both *Antronicippe serrata* Stock & Iliffe, 1990 (family Pardaliscidae) and *Valettietta cavernicola* Stock & Iliffe, 1990 (family Lysianassidae) belong to families with predominantly deep-sea members. Additionally, *Antronicippe* is closely related to *Spelaeonicippe,* a genus with two species inhabiting anchialine caves in the Canary Islands and West Indies. The epacteriscid copepod *Enantiosis,* a genus containing only anchialine or crevicular members, is represented by a species most closely related to an anchialine form from Bermuda (A. Fosshagen, pers. comm.). A caridean shrimp collected from the deepest sections of the cave may belong to the genus *Parhippolyte,* an anchialine group widely distributed in the tropical Indo-Pacific (A. J. Bruce, pers. comm.).

Considering the nature of the habitat from which *Guitonia troglophila* was collected, it is likely that this crab is restricted to similar anchialine environments within the Galápagos. Grieta de Caleta la Torta was one of the richest collecting sites found in these islands in terms of numbers of troglobic taxa. At least 8 other obligate anchialine taxa, including 3 species of amphipods, 2 ostracods, 2 shrimps, and a copepod were found there. The presence of such a rich and diverse obligate anchialine fauna testifies to the isolation of this grieta from the sea and its suitability as a habitat for anchialine species. The fact that some light penetrates into the shallower waters of the pool during the day is not significant, as anchialine shrimps are elsewhere commonly found in illuminated, but land-locked pools (see Holthuis 1973), although they regularly disappear into, and are apparently dispersed through, lightless subterranean channels.

Acknowledgments

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DESCRIPTION OF A NEW *AXIANASSA* (CRUSTACEA: DECAPODA: THALASSINIDEA) FROM BRAZIL, AND ITS FIRST LARVAL STAGE

Sérgio de A. Rodrigues and Roberto Munehisa Shimizu

Abstract.—A new species of laomediid mud shrimp, *Axianassa australis* is described from the Brazilian coast. The species is characterized by possessing a long dagger-like antennal acicle with a tooth on the mesial margin, a small tooth on the basis of maxilliped 3 and a spiniform process on abdominal somite 1. The larva has a smooth carapace, abdominal segment 5 with a pair of lateral spines, mandibles asymmetrical and sickle-shaped, endopod of maxillule and maxilla unsegmented, maxillipeds with exopods 2 segmented, maxilliped 3 without endopod, telson spatuliform and with spine 2 reduced.

Schmitt (1924) established the genus *Axianassa* for *A. intermedia* based on specimens from Curaçao, Lesser Antilles, and later (Schmitt 1936) registered the presence of the same species at Aruba. In the interim Boone (1931) described a second species, *A. mineri,* from the Pacific coast of Panama. Due to the cryptic way of life of these fossorial crustaceans no other records of *Axianassa* appeared in the literature until the recent descriptions by Kensley & Heard (1990) of *A. arenaria, A. canalis* and *A. jamaicense* from the Gulf of Mexico, the Panama Canal and Jamaica, respectively. These authors also reexamined all the nine specimens deposited in North American collections and redescribed *A. intermedia* and *A. mineri.*

A new species is here described from the coast of Brazil, based on material collected at Valença, Estado da Bahia, and São Sebastião, Estado de São Paulo (Rodrigues & Shimizu 1987). Several specimens were obtained alive from the latter locality with the help of a suction device (Rodrigues 1966) similar to the "yabby pump" developed in Australia (Hailstone & Stephenson 1961). One ovigerous female was maintained in an aquarium inside an artificial burrow (Rodrigues 1983, Rodrigues & Hödl 1990) until the hatching of the larvae. The larvae hatched as pre-zoea and in a few hours shed the embrionic skin to become a free swimming zoea. These larvae were placed in Petri dishes with water from the collection site and fed *Artemia* nauplii. Only one larva reached the second stage, dying soon thereafter. As the larvae of *Axianassa* species hatched from eggs have not been previously described, a description of the first larval stage of *A. australis,* new species is here included to provide more information for the controversial question of thalassinidean phylogeny (Saint Laurent 1973, 1979; Poore & Griffin 1979, Kensley & Heard 1990).

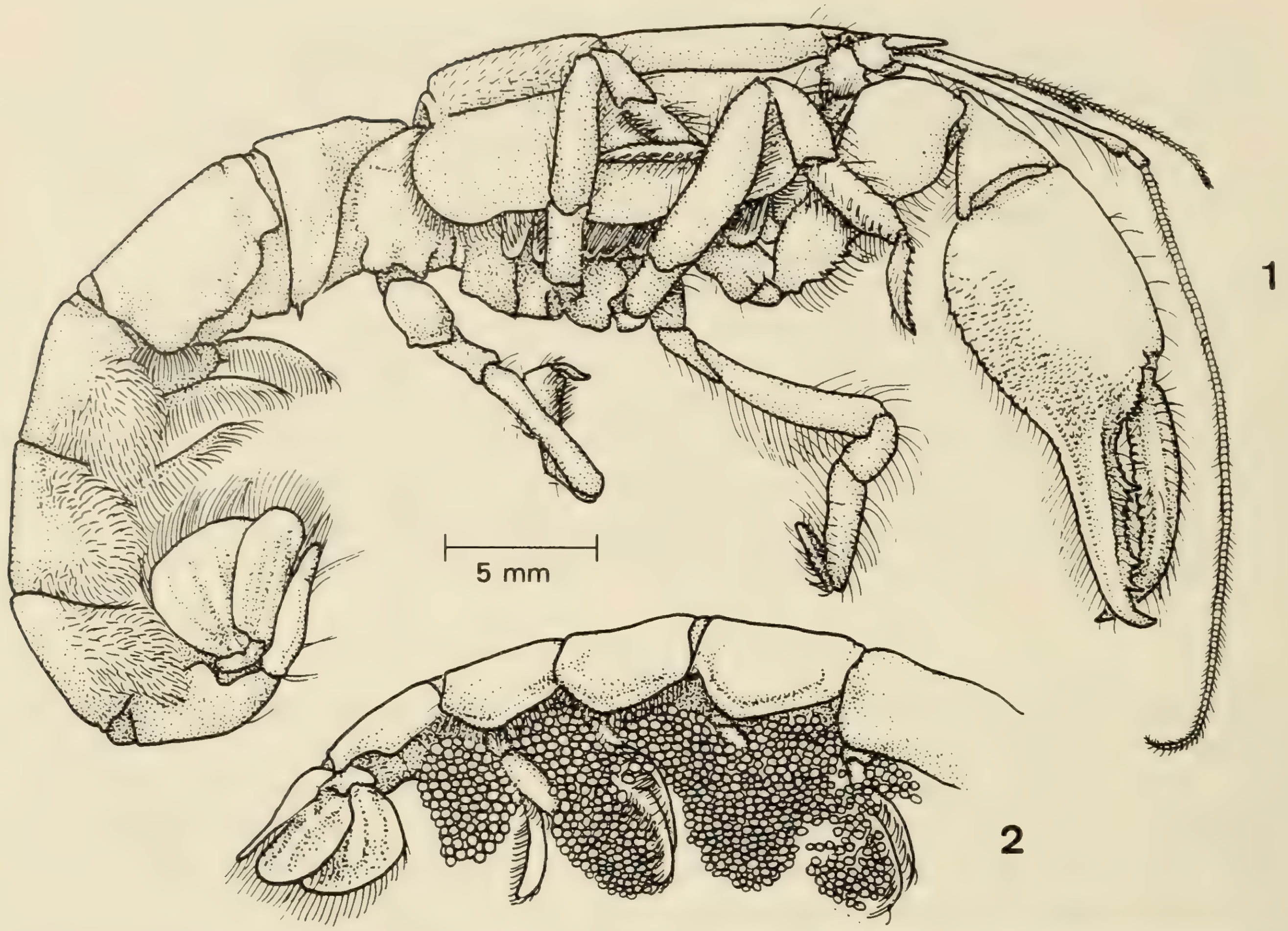
The holotype has been deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP) and paratypes are in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM) and the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RMNH).

Family Laomediidae

Axianassa australis, new species

Figs. 1–20

Material.—Holotype, MZUSP 105841, 1 ♂ cl 13.4 mm; USNM, 1 ♂ cl 14.2 mm, Fa-



Figs. 1, 2. *Axianassa australis,* new species, paratypes: 1, ♂, in lateral view; 2, ♀, abdomen with eggs in lateral view.

zenda Maricultura, Valença, Bahia, Brazil, intertidal, taken from mangrove mud during the digging of a shrimp pond, coll. S.L.S. Bueno, Mar 1983. USNM 243485, 1 ♂ cl 7 mm, 1 ♀ cl 6.1 mm; RMNH 37697, 1 ♀, not measured; RMNH 37698, 1 ♂, not measured; Praia do Araçá, São Sebastião, São Paulo, Brazil, intertidal, taken from burrow in muddy sand with yabby pump, coll. S. A. Rodrigues and R. M. Shimizu, May 1985.

Description.—Carapace with linea thalassinica and cervical groove clearly defined; rostrum anteriorly rounded, reaching beyond cornea of eyes (Figs. 1, 3). Abdomen thin-walled, tergites bearing minute spiniform hairs; somite 1 somewhat longer than somite 2 and about as long as somites 3–6, pleuron produced ventrally into small but strong spiniform process; somite 2 with postero-lateral margins bearing dense tuft of plumose setae; somites 3–5 with very dense lateral fringes of plumose setae; somite 6 almost naked, ventral margins sinuous (Figs. 1, 2). Telson length slightly less than greatest width; broadly rounded posteriorly, bearing long plumose setae (Figs. 1, 2, 20).

Cornea not clearly demarcated from eyestalk, moderately pigmented. Article 3 of antennular peduncle slender, elongate-cylindrical, about twice combined length of articles 1 and 2; ventral flagellum slightly more than ⅓ length of dorsal flagellum; latter reaching slightly beyond tip of antennal peduncle (Fig. 3). Antennal acicle slender, dagger-like, with small sharp tooth on mesial margin; peduncle article 4 slender, elongate-cylindrical, bearing long and short scattered setae along its length; flagellum reaching beyond tip of chelipeds (Figs. 1, 3).

Mouthparts as illustrated. Mandible (Fig. 4) with 8 cusps on cutting edge; palp 3-segmented; articles 2 and 3 each bearing 5 plumose setae. Maxilla 2 (Fig. 6), scaphognathite bearing 7 elongate setae on posterior margin. Maxilliped 1 (Fig. 7), endopod and proximal part of exopod paddle-shaped; exopod 3-segmented. Maxilliped 2 (Fig. 8) typical of genus. Maxilliped 3 (Fig. 9), basis with 1 or 2 (in large specimens) small teeth on lateral surface; dentate crest of ischium bearing 14 teeth; merus, carpus and propodus with bands of fusiform setae.

Pereopods 1 (Figs. 10–13) asymmetrical, sexually dimorphic. Males (Figs. 12, 13) with ventral margin of ischium bearing 3–6 sharp teeth; ventral margin of merus obscurely denticulated; carpus of larger chela with vestigial tubercle ventrodistally; dactylus of larger chela shorter than palm, both fingers with inconspicuous and rounded teeth; dactylus of smaller chela longer than palm, cutting edge bearing row of small rounded teeth; fixed finger with many small and 3 large canine-like teeth. Females (Figs. 10, 11) with ventral margin of ischium bearing 3 sharp teeth; merus and carpus smooth; larger chela with dactylus about as long as palm, fixed finger with many small and 2 large canine-like teeth.

Pereopod 2 (Fig. 14), merus, carpus and propodus bearing elongate setae on posterior margins; dactylus armed with row of fine spinules on posterior margin. Pereopod 3 (Fig. 15) and 4 (Fig. 16) similar; propodus with posterodistal band of stiff setae; dactylus sickle-shaped with row of 9–14 strong corneous spines on posterior margin, anterior margin bearing row of fine spinules. Pereopod 5 (Fig. 17) sub-chelate, propodus with long grooming apparatus on inner face; dactylus flattened, with row of tiny spinules along posterior margin.

Pleopod 1 of males absent; of females (Fig. 18) slender, 2-segmented, terminal segment with crenulated margins. Pleopods 2–5 (Fig. 19) similar, endopod and exopod oval-shaped.

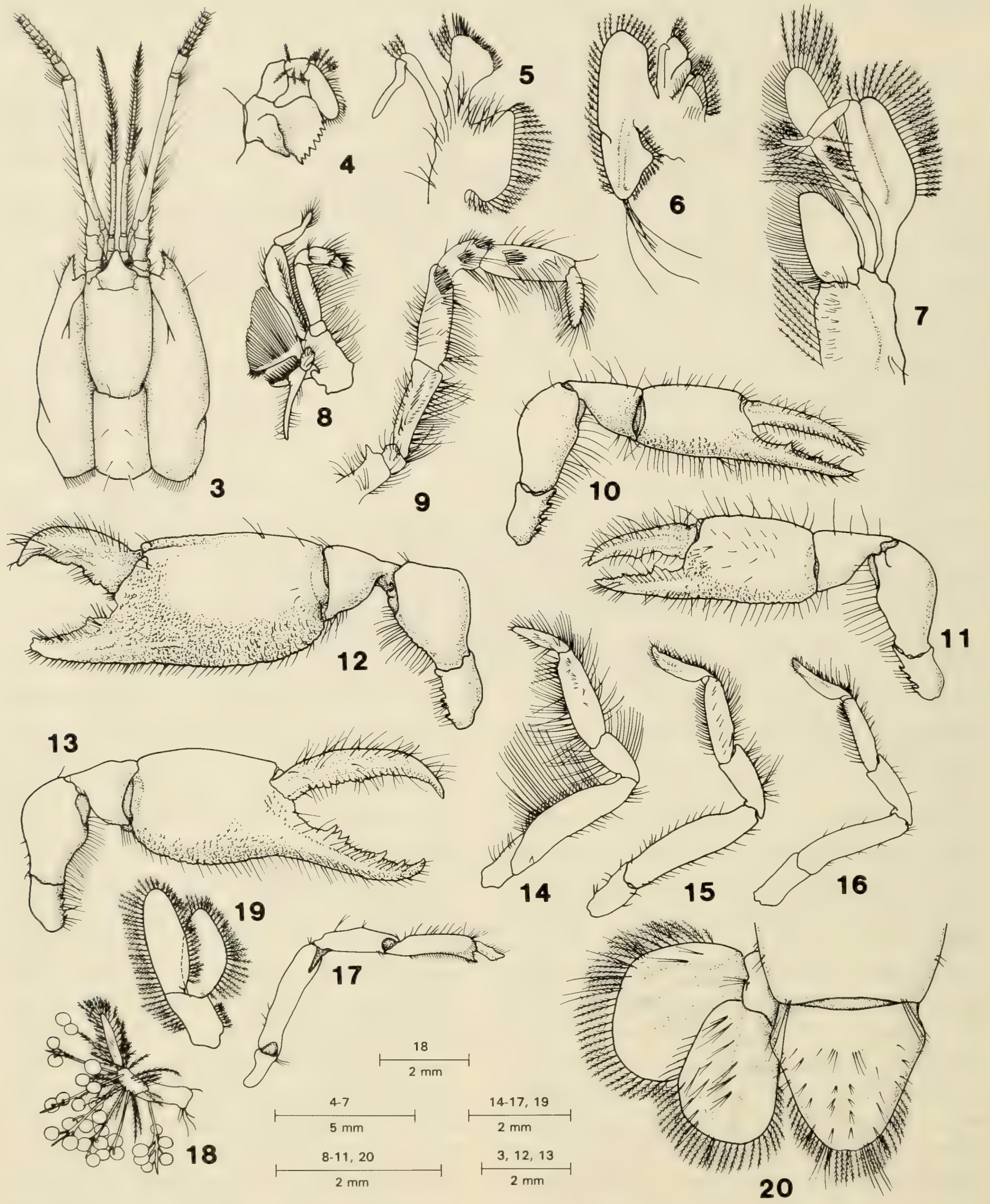
Uropodal rami broadly ovate, margins without spines, dorsal surfaces with scattered minute spinules, visible only under high magnification.

Gill formula as in type species of genus (Kensley & Heard 1990).

Coloration.—Both sexes have a salmon-pinkish body and pale yellowish pereopods and antennae.

Etymology.—The specific name refers to the South, as this is the first species of the genus to be reported from the Southern Hemisphere.

Discussion.—*Axianassa australis* is closely related to *A. canalis* considering the long, dagger-like shaped antennal acicle (short and apically bifid in *A. mineri*) with a tooth on the mesial margin (lacking in *A. arenaria*), and the spiniform process of abdominal somite 1 (absent in *A. jamaicense* and *A. intermedia*). However, *A. australis* differs from *A. canalis* in the following characters: in *A. canalis* the article 4 of antennal peduncle bears a row of short spinules along the ventral surface and in *A. australis* long and short scattered setae; in *A. canalis* the maxilliped 3 has a strong tooth on the basis and a band of fusiform setae on the posterior margin of the ischium, while in *A. australis* this appendage bears 1 or 2 (in the larger specimens) small teeth on the basis and no band of fusiform setae on the ischium; examination of the type specimen of *A. canalis* revealed the presence of two small posterolateral corneous spinules on the coxae of pleopods 2–4 that were not mentioned in the original description, these spinules being absent in *A. australis*; the single marginal tooth on the lateral margin of the outer uropodal ramus of *A. canalis* is not found in *A. australis*; the minute spinules scattered over the surface of the abdominal tergites of *A. australis* are absent in *A. canalis.* As the first pereopods of *A. canalis* are missing



Figs. 3–20. *Axianassa australis*, new species. 3–9, 12–17, 19, 20, holotype; 10, 11, 18, paratype. 3, carapace in dorsal view; 4, mandible; 5, maxilla 1; 6, maxilla 2; 7, maxilliped 1; 8, maxilliped 2; 9, maxilliped 3, inner view; 10, pereopod 1, smaller cheliped of female; 11, pereopod 1, larger cheliped of female; 12, pereopod 1, larger cheliped of male; 13, pereopod 1, smaller cheliped of male; 14, pereopod 2; 15, pereopod 3; 16, pereopod 4; 17, pereopod 5; 18, pleopod 1 of female with eggs; 19, pleopod 2–5; 20, telson and left uropod in dorsal view.

in the only existing specimen, other differences may also be found, as these legs are usually species-specific in proportions and armature.

Habitat.—In both collecting sites, *A. australis* was found in poorly oxygenated muddy sediment of very sheltered areas near mangrove vegetation. At São Sebastião the population is small, restricted to an area of about 100 × 50 m and is situated nearly 300 m from the type locality of *Callichirus guassutinga* (Rodrigues, 1971) and *C. guara* (Rodrigues, 1971). For further information see the remarks on the habitat of *C. guassutinga* in Rodrigues (1971).

First Larval Stage
Figs. 21–32

Total length around 3 mm. Body laterally compressed, transparent except for orange chromatophore on middle anterior portion of carapace and dark pigment of eyes.

Carapace (Figs. 21, 22) smooth; without teeth, serrations, linea thalassinica or cervical groove; rostrum smooth and straight, about as long as antennae.

Abdomen (Figs. 21, 22) 5-segmented, somite 5 bearing pair of large lateral spines, somite 6 fused with telson.

Eyes (Figs. 21, 22) rounded, sessile.

Antennule (Fig. 23) unsegmented; distal extremity with 3 aesthetascs and 2 smooth setae. Antenna (Fig. 24), exopod with 1 spine and 10 setae, endopod with 3 apical setae, protopod without spine.

Mandibles (Figs. 25, 26) asymmetrical, sickle-shaped, left much more slender than right. Maxillule (Fig. 27), endopod unsegmented with 3 apical setae, protopodal endites each with 4 setae. Maxilla (Fig. 28), scaphognathite with 5 setae; endopod small, unsegmented, with 2 setae; protopodal endites each with 4 setae.

Maxilliped 1 (Fig. 29), exopod 2-segmented, with 4 apical setae; endopod with 4 segments, bearing 4,1,0,1 setae from distal to proximal; protopod with 3 setae on mesial margin and 2 on lateral. Maxilliped 2 (Fig. 30), exopod 2-segmented with 4 apical setae and 3 on the lateral margin; endopod 4-segmented, terminal segment with 3 apical and 2 lateral setae, subterminal segment with 3 setae; protopod naked. Maxilliped 3 (Fig. 31), exopod 2-segmented, without setae; endopod absent.

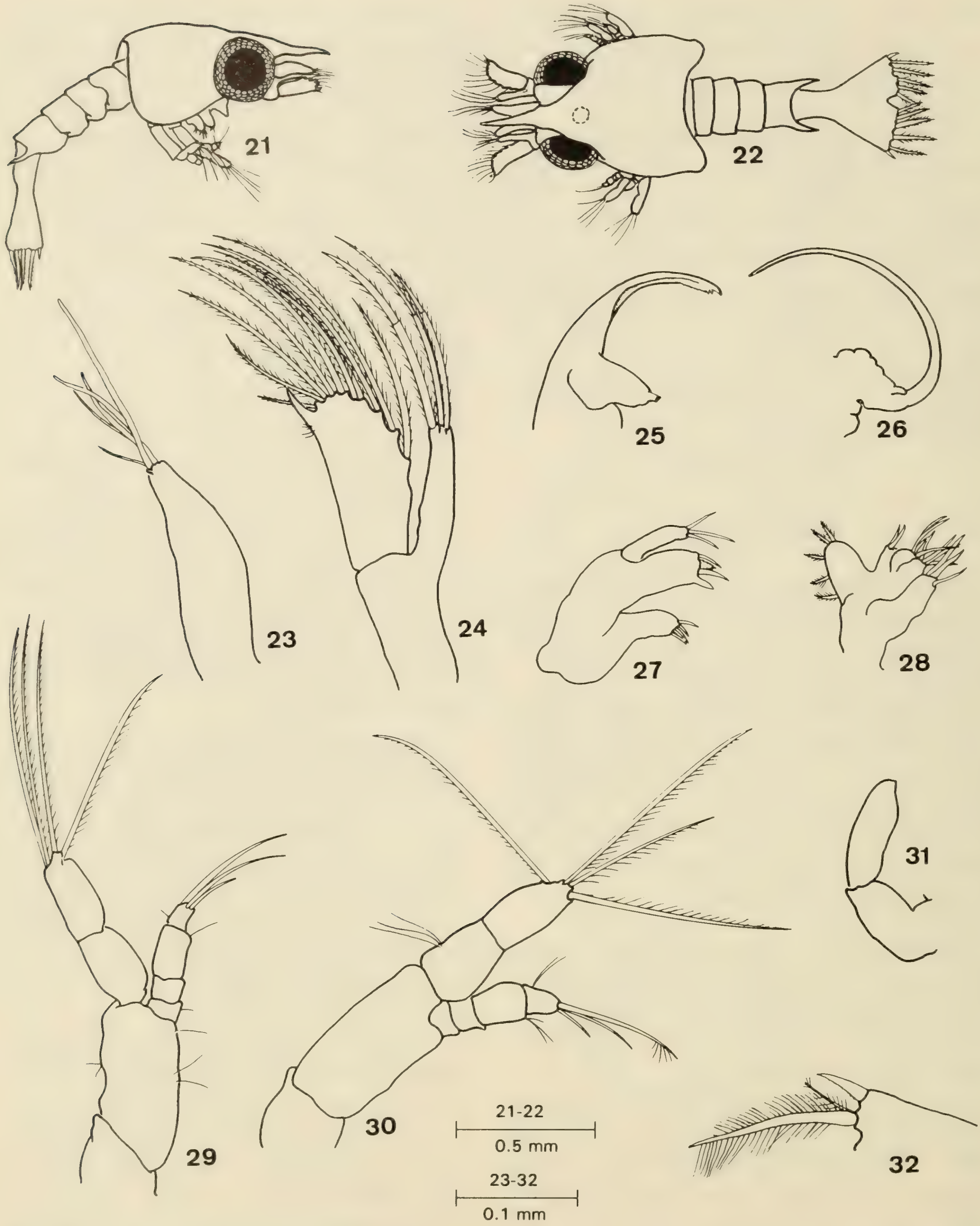
Pereopods lacking.

Telson (Fig. 22) spatuliform, with median sinus and 7+7 spines, spine 2 (Fig. 32) reduced to a hair.

Remarks.—Ngoc-Ho (1981) described the larval stages of a species belonging to the family Laomediidae from the Gulf of Mexico tentatively attributed to the genus *Axianassa.* The similarity of this larva with the one of *Axianassa australis* here described is striking, and there is no doubt that it belongs to the genus *Axianassa.* However, the species is not the same as there are differences in the proportion and number of setae in several appendices.

The laomediid larva described by Gurney (1938) as D.I., was collected off the northeastern coast of Brazil (10°20′S; 34°54′W) not very far from the northern known distribution of *A. australis.* The first stage of D.I. differs from the larva of *A. australis* in having one small spine on the basis of the antenna and a rudimentary pereopod 1. The generic identification of this larva remains unknown (Ngoc-Ho 1981).

The genus *Axianassa* has been placed in a separate family (Axianassidae) or included in the family Laomediidae, and its taxonomic position is still in debate. A complete review of the subject was recently presented by Kensley & Heard (1990), and Konishi (1989) compared the main zoeal characters among the five thalassinidean families. The identification of the larva of *A. australis,* with unquestionable laomediid characters such as the asymmetrical and sickle-shaped mandibles, the segmented endopods of maxillule and maxilla, and the absence of



Figs. 21–32. *Axianassa australis,* new species, first larval stage: 21, whole body in lateral view; 22, whole body in dorsal view, dotted circle marks the position of the chromatophore; 23, antenna 1; 24, antenna 2; 25, left mandible; 26, right mandible; 27, maxilla 1; 28, maxilla 2; 29, maxilliped 1; 30, maxilliped 2; 31, maxilliped 3; 32, telson spines 1–3.

endopods on maxilliped 3, provides additional evidence for placement of the genus *Axianassa* in the family Laomediidae.

Acknowledgments

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TWO NEW CALLIANASSID SHRIMPS FROM BRAZIL (CRUSTACEA: DECAPODA: THALASSINIDEA)

Sérgio de A. Rodrigues and Raymond B. Manning

Abstract.—*Biffarius delicatulus* and *Eucalliax cearaensis* are described from Brazil. Each species is the third of their genus to be recorded from the western Atlantic and the first of their genus known from South America.

Among the unstudied callianassids accumulated by the senior author since his review of the Brazilian callianassids (Rodrigues 1971) are two previously undescribed species. One of these is referable to the genus *Biffarius* and the other to *Eucalliax*; both of these genera were recently erected for American species by Manning & Felder (1991).

The holotypes have been deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP) and paratypes are in that collection and in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Carapace length (cl) is postorbital carapace length in millimeters (mm). Other abbreviations used include: A1, antennule; A2, antenna; leg., collector; m, meters; Mxp1–3, maxillipeds 1–3; P1–5, pereopods 1–5; Plp1–5, pleopods 1–5.

Biffarius delicatulus, new species

Fig. 1

Material.—Brazil, State of São Paulo: São Sebastião, Praia de Enseada [city of São Sebastião = 23°40′S, 45°20′W], dug from sand at low tide, 3 Jun 1981, leg. S. Rosso: 1 ♂, cl 3.8 mm (paratype, USNM 252546).—São Sebastião, Praia do Araça, collected in sand at low tide with yabby pump, 18 May 1985, leg. S. A. Rodrigues: 6 ♂, cl 4.0–6.8 mm, 2 ♀, cl 4.3, 4.4 mm (1 ♂ is holotype, MZUSP 10582; other specimens are paratypes, MZUSP (uncat.) and USNM 252547).

Diagnosis.—Size very small, cl less than 7 mm in adults. Telson subquadrate, unarmed. Mxp3 ischium-merus operculiform, without exopod, inner surface without crest or teeth. Male with one form of cheliped, merus of both chelipeds with ventral hook. Plp2 of male small, uniramous. Uropods unarmed.

Description.—Carapace smooth, with dorsal oval, without cardiac prominence, cervical groove distinct, linea thalassinica distinct, parallel to longitudinal axis of body; rostrum short; lateral frontal projections absent.

Abdominal somites smooth, somite 1 saddle-like, shorter than others; somite 2 longer than others, with small tuft of setae on posterolateral margin; somites 3–5 subequal in length, each with small lateral row of setae; somite 6 about as long as telson, with small posterolateral rows of setae. Telson subquadrate, slightly wider than long, with 1 tuft of setae on mid-dorsal surface, 2 other tufts near extremities of distal margin.

Eyes flattened, slightly convex, about as long as first segment of A1 peduncle, external margins moderately convergent, mesial margins parallel up to level of cornea, there divergent towards pointed tips; cornea rounded, darkly pigmented, subterminal.

A1 peduncle reaching slightly beyond tip of penultimate segment of A2 peduncle; segment 3 twice as long as segment 2, segment 1 a little longer than segment 2; flagellum shorter than peduncle. A2 peduncle with segment 4 slightly shorter than segment 3

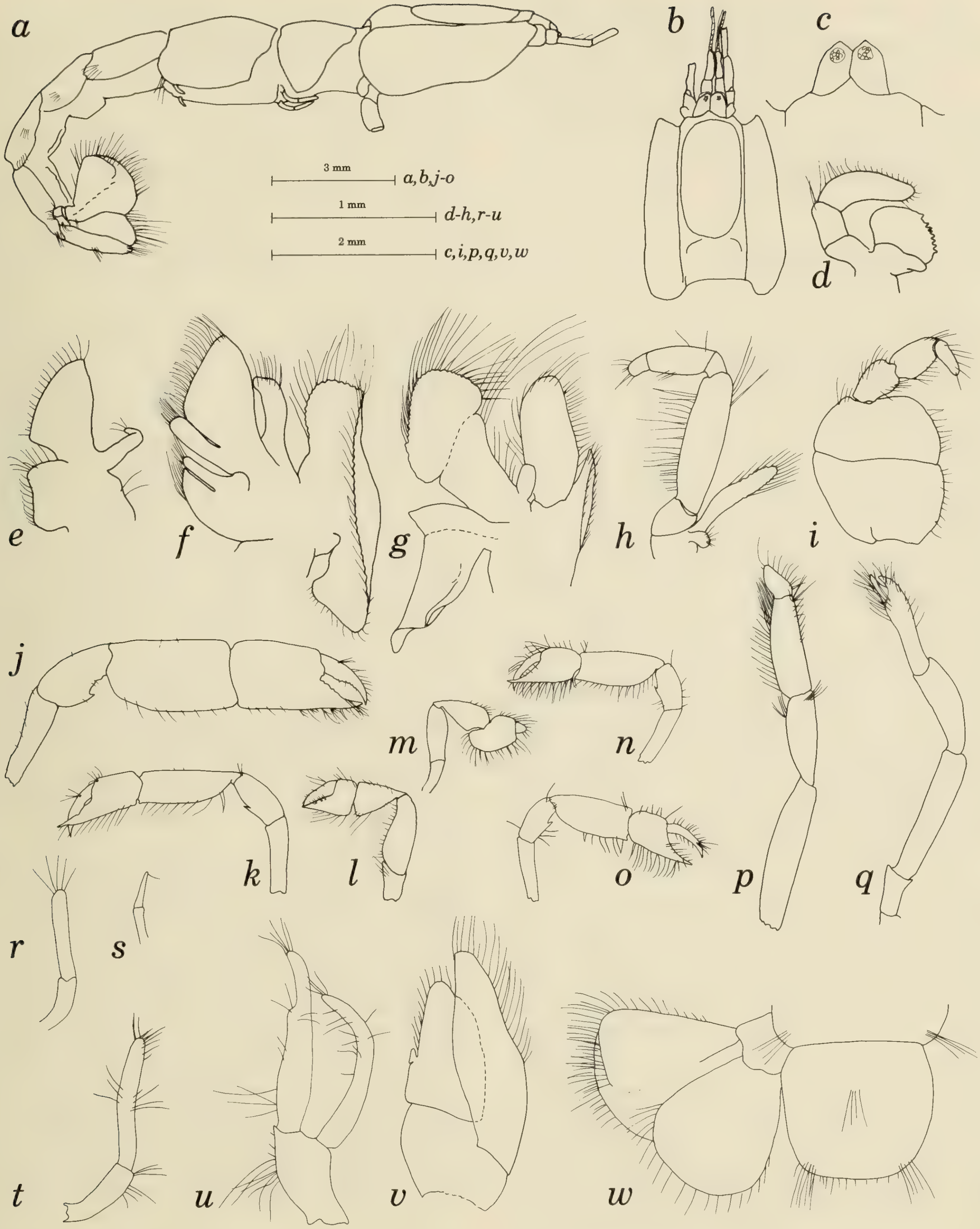

Fig. 1. *Biffarius delicatulus,* new species. a, Lateral view; b, Carapace and anterior appendages; c, Front and eyes; d, Mandible; e, Maxilla 1; f, Maxilla 2; g, Mxp1; h, Mxp2; i, Mxp3; j, Major cheliped of male; k, Minor cheliped of male; l, P2; m, P3; n, Left cheliped of female; o, Right cheliped of female; p, P4; q, P5; r, Male Plp1; s, Male Plp2; t, Female Plp1; u, Female Plp2; v, Plp4; w, Telson and left uropod. a–m, p–s, v–w, male paratype, cl 4.0 mm; n–o, t–u, female paratype, cl 4.3 mm.

Table 1.—Gill formula of *Biffarius delicatulus.*

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	—	—
Arthrobranchs	—	—	2	2	2	2	2	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	—	—	—	—	—	—

and as long as segment 1 and 2 together; antennal scale small; flagellum about 3 times longer than peduncle.

Mandible with 7 sharp teeth on incisor process; molar process unarmed; palp 3-segmented, segment 3 longer than segments 1 and 2 combined. Maxillule with broad protopodal endites; palp slender, with curved tip. Maxilla with protopodal endites bilobed; palp slender, reaching slightly beyond middle of basal endite; exopod broad, with crenulated margins bearing equally-spaced setae, longer on distal margin. Mxp1 with protopodal endites as illustrated (Fig. 1g); palp small but distinct, longer than wide; exopod appearing articulated, distal portion with crenulated margin bearing long setae; epipod divided by constriction, anterior portion short and truncate, posterior portion produced into curved lobe. Mxp2 with endopod 5-segmented, as illustrated (Fig. 1h); exopod unsegmented, shorter than endopodal merus; protopod with small setose exopod, lacking arthrobranch. Mxp3 ischium-merus operculiform; ischium 1.5 times wider than long, mesial surface with sparse small setae, without crest or teeth; merus 2 times wider than long, proximal margin as long as distal margin of ischium, 4 times wider than carpus and prodopus; propodus longer than wide, only slightly wider than digitiform dactylus.

Larger cheliped of male with ischium smooth, unarmed; merus with anterior margin smooth, posterior margin produced into distally directed hook and with distal portion serrated; carpus about 1.5 times longer than wide; palm shorter than carpus, slightly longer than wide; fingers shorter than palm, gaping, tips acutely pointed, cutting edges minutely serrated. Smaller cheliped of male with ischium smooth, merus usually with small, acute hook at midlength of posterior margin (absent in 1 specimen); carpus longer than other joints, length about 3 times width; propodus widening distally; fingers subequal, curved, longer than palm, sharply pointed, with some serrations on cutting edges. Females with both chelipeds of same size and shape, differing from small cheliped of male only in setation and proportions of carpus (2.2 rather than 3 times longer than wide).

P2 with fingers not gaping, cutting edges straight, smooth. P3 with ischium and merus of about same width, merus longer than ischium; carpus broadening distally; propodus wider than carpus, anterior and posterior margins convex, posterior margin much longer than anterior; dactylus as long as wide, with rounded tip. P4 with posterior margin of propodus bending towards dactylus, lacking subchelar projection. P5 distinctly chelate, fingers small, tips curved.

Branchial formula, differing from normal callianassid formula in complete absence of arthrobranch on Mxp2, as shown in Table 1.

Plp1 of male uniramous, 2-segmented; distal segment spatulate, with 5 long apical setae. Plp2 rudimentary, uniramous, 2-segmented; distal segment with 1 short apical seta. Plp1 of female uniramous, 2-segmented; proximal segment with a few subterminal short setae; distal joint about 2 times longer than proximal, with about 12 small setae at midlength, 4 small subterminal slender setae, and 4 spiniform apical setae. Plp2 of female biramous; endopod straight, with 5 terminal setae and a few setae scattered along its length; exopod similar to endopod but curved. Plp3–5 with stubby, projecting appendices internae in both sexes.

Uropodal endopod widening to its distal extremity, about as long as broad, marginal setae delicate; exopod slightly longer than endopod, upper plate incomplete, distal margin convex, without strong setae.

Etymology.—From the Latin, *delicatus,* delicate, as, like *B. biformis* and *B. fragilis,* specimens are very easily damaged when handled.

Remarks.—This species resembles *B. biformis* (Biffar, 1971) and *B. fragilis* (Biffar, 1970), the only other species assigned to the genus, but differs from both in having vestigial pleopods on the second abdominal somite of the male. It further differs from *B. biformis* in lacking spinules on the posterolateral corner of the telson and in having only one form of major cheliped in the male. It differs from *B. fragilis* in having a weak hook on the merus of the smaller cheliped, a relatively short antennular peduncle, and no spinules on the inner face of the ischium of the third maxilliped. As in *B. biformis,* the female of *B. delicatulus* lacks a major cheliped—both chelipeds are of the same size and shape. All three species lack an arthrobranch on the second maxilliped.

Eucalliax cearaensis, new species
Fig. 2

Material.—Brazil, State of Ceará: Fortaleza [3°45′S, 38°35′W], Barro de Ceará, right bank of river mouth, collected in sand at low tide with yabby pump, 21 Feb 1984, leg. S. A. Rodrigues: 2 ♂, cl 7 mm, 3 ♀, cl 6–7.2 mm (1 male is holotype, MZUSP 10583; other specimens are paratypes, USNM 252546).

Diagnosis.—Rostrum short, not spined. Carpus of chelipeds lacking distal acute projections or spines. Male Plp1 terminating in single hook.

Description.—Carapace about ⅓ as long as body, lacking cardiac prominence, dorsal oval, rostral spine, and rostral carina, cervical groove indistinct, present as suture; dorsal midline with 2 small rounded pits, one on anterior portion of gastric area, other on caudal portion of cardiac area; linea thalassinica parallel to midline of body; rostrum short; lateral frontal projections of carapace inconspicuous. Abdominal somites smooth, somite 1 shortest, somite 2 longest; somites 3–5 subequal in length, each with small lateral row of setae. Telson distinctly broader than long, subquadrate, unarmed.

Eyes flattened, extending slightly beyond distal margin of first segment of A1, almost 2 times longer than wide; external margins convergent, internal margins parallel for most of length, diverging near pointed tips; cornea distinct, darkly pigmented, subterminal.

A1 peduncle about as long as A2 peduncle; segment 1 shortest, segment 3 longest; antennular flagellum about 1.5 times longer than peduncle. Antennal scale absent; antennal flagellum about 5 times as long as peduncle.

Mandible with molar process smooth, incisor process with about 10 small, unequal teeth; mandibular palp 3 segmented, segment 3 larger than the preceding and bearing many stiff setae. Maxillule with many short spiniform setae on mesial margin of protopodal endite; palp slender, curved, unsegmented. Maxilla with protopodal endites bilobed, mesial margins bearing numerous slender setae; palp about as long as endites; exopod broad with anterior and posterior margins rounded.

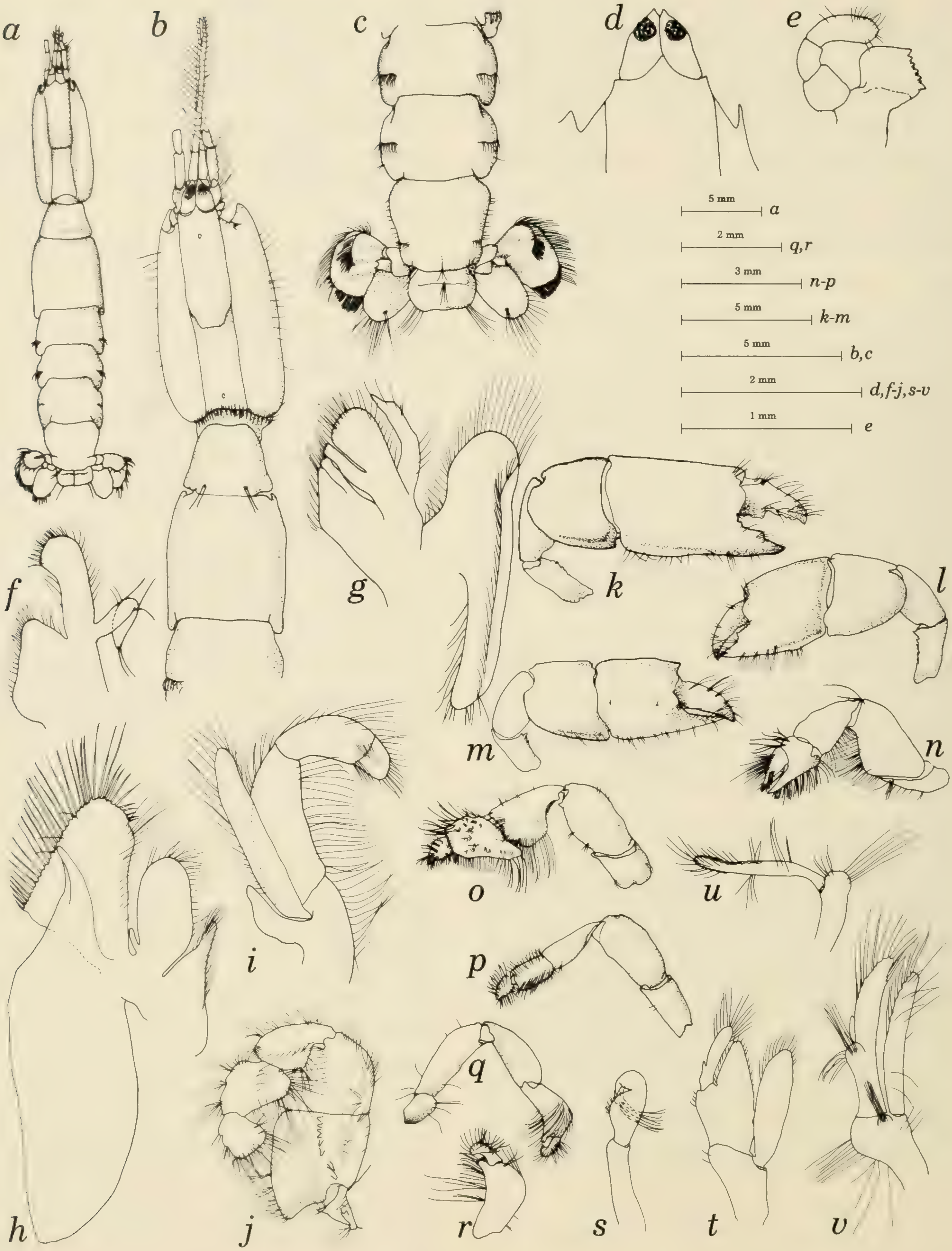

Fig. 2. *Eucalliax cearaensis,* new species. a, Dorsal view; b, Carapace, frontal appendages, and anterior abdominal somites; c, Posterior part of abdomen and tail fan; d, Front and eyes; e, Mandible; f, Maxilla 1; g, Maxilla 2; h, Mxp1; i, Mxp2; j, Mxp3; k, Right cheliped of male; l, Left cheliped of female; m, Right cheliped of female; n, P2; o, P3; p, P4; q, P5; r, P5 propodus and dactylus; s, Male Plp1; t, Male Plp2; u, Female Plp1; v, Female Plp2. a–k, n–t, male paratype, cl 7 mm; l–m, u–v, female paratype, cl 6 mm.

Table 2.—Branchial formula of *Eucalliax cearaensis* (r = rudimentary).

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	—	—
Arthrobranchs	—	r	2	2	2	2	2	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	—	—	—	—	—	—

Mxp1 with coxa triangular, base rounded; palp short and narrow; exopod unsegmented; epipod large, tapering anteriorly, broadening posteriorly. Mxp2 with pediform endopod; exopod slightly longer than half of endopod; protopod with small leaf-like epipod. Mxp3 with ischium-merus subpediform, length about twice merus width; ischial ridge with about 8 denticles; carpus oval; propodus about as broad as carpus, broader proximally than distally; dactylus blunt, ovate, about as long as wide.

Branchial formula as shown in Table 2.

Chelipeds subequal, slightly sexually dimorphic. Large cheliped of male with row of spines on ischium increasing in size distally; merus unarmed, about 2 times longer than wide; carpus shorter than merus, about as long as wide, anterior and posterior margins distally rounded, without acute projections; palm longer than wide, margins smooth; fixed finger strong, blunt at tip, much shorter than dactylus, cutting edge with median triangular tooth; dactylus blunt, curving inward distally, cutting edge with strong proximal tooth and 3 small teeth diminishing in size distally. Larger cheliped of female with ischium, merus, and carpus as in male; palm as long as wide, fixed finger with rather sharp teeth; dactylus with acute tip, cutting edge slightly serrated near proximal extremity. Smaller cheliped with merus, carpus, and palm as in larger cheliped of female; fingers with acute tips and nearly smooth cutting edges.

P2 with ischium small, wider than long; merus the widest joint, narrowing distally; palm wider than long; fingers with pointed tips, cutting edges straight, not gaping. P3 with ischium as wide as merus; merus subcylindrical, tapering to articulation with carpus; carpus widening near midlength; posterior margin of propodus with small lobe proximally, anterior margin convex. P4 simple, ischium and merus about as long as carpus, propodus and dactylus combined; merus the widest joint, carpus slender, propodus and dactylus with dense tufts of setae. P5 chelate, ischium and merus shorter than combined lengths of carpus, propodus and dactylus; carpus and propodus the widest joints; propodus and dactylus with dense tufts of setae; fixed finger spoon-shaped; dactylus curved.

Plp1 of male uniramous, 2-segmented; distal segment with flattened, curved tip bearing marginal row of long setae, posterior margin convex at midlength, with row of minute setae; proximal segment longer than distal, smooth, with tuft of short setae near distal extremity of posterior margin. Plp2 of male biramous, exopod and endopod leaf-like; endopod 3-segmented, proximal segment with inner projection almost as long as distal segment; latter narrow, with small appendix interna. Plp1 of female uniramous, 2-segmented, distal segment articulated to distal portion of anterior margin of proximal segment, forming an angle of 90° with it, distal extremity flattened, with long marginal setae; proximal segment with group of long and group of short setae on dilated distal portion of posterior margin. Plp2 of female biramous, exopod and endopod narrow, spatulate, with distal half bearing long marginal setae; endopod with knob near midlength of inner margin, adjacent to appendix interna, bearing a rod-like tuft of long setae; protopod with similar tuft of setae near distal margin, almost between exopod and endopod, and with stronger tuft of setae on anterior surface. Plp3–5 with finger-like appendices internae in both sexes.

Uropodal endopod oval, about 1.5 times longer than wide, distal tip extending well beyond posterior margin of telson, margins with widely spaced setae, dorsal surface with tuft of long setae near distal extremity of mesial margin; exopod about as long as endopod, upper plate distinctly shorter than lower plate, with double row of about 14 spiniform setae on mesial portion of distal margin, lower plate with single row of 12 spiniform setae on central part of distal margin, increasing in size medially.

Etymology.—The specific name is derived from the State of Ceará which contains the type locality.

Remarks.—Two species of *Eucalliax* have been described from the American tropical Atlantic: *E. quadracuta* (Biffar, 1970) and *E. jonesi* (Heard, 1989). This new species differs from both in having the A1 and A2 peduncles subequal in length. It further differs from *E. quadracuta* in lacking acute distal processes or spines on the dorsal and ventral margins of the carpus of the chelipeds, in having a row of spiniform setae on the uropods, and in the shape and setation of Plp1–2 in the male which in *E. quadracuta* is a simple spatulate lobe, not recurved into a distal hook. *Eucalliax cearaensis* resembles *E. jonesi* in the smooth carpus of the chelipeds and the presence of spiniform setae on the uropods, but differs in having a much shorter rostral spine and in having the male Plp1 terminating in a single apical lobe rather than in two lobes.

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MESOCYCLOPS GUANGXIENSIS, NEW SPECIES, AND NEW RECORDS OF FOUR CONGENERS (CRUSTACEA: COPEPODA: CYCLOPIDAE) FROM CHINA, LAOS, AND VIET NAM

Janet W. Reid and Brian H. Kay

Abstract.—Five species of *Mesocyclops* are reported from China, Laos, and Viet Nam. Four of these, *M. ogunnus,* from Laos, *M.* cf. *pehpeiensis,* from Laos, *M.* cf. *thermocyclopoides,* from Viet Nam, and *M. thermocyclopoides acutus,* from Laos, can be referred, although provisionally in two cases, to previously described species. One, *M. guangxiensis,* collected in China, Laos, and Viet Nam, is new to science. New microcharacters useful in the taxonomy of *Mesocyclops* are spine patterns on the antennule, mandible, maxilla, leg 4 coxa-basipodite, and leg 6 plate.

The Asian species of cyclopoid copepods of the genus *Mesocyclops* are incompletely known. Therefore it is not surprising that collections from a few localities in China, Laos, and Viet Nam by one of us (BHK) and associates included several species of uncertain taxonomic placement and one that is new to science. This article lists the species, discusses the probable affinities of several, and describes the new species.

Methods

The specimens were fixed in 5% formalin and transferred to 70% ethanol for long-term storage. For taxonomic determination, specimens were placed in a solution of 70% ethanol-10% glycerin which was allowed to evaporate to nearly pure glycerin. Specimens were examined either in glycerin or in lactic acid, and some were mounted permanently either in commercial glycerin jelly or in polyvinyl lactophenol (PVL) with a little chlorazol black E added. Measurements were made in glycerin. Drawings were made by means of a Wild M50 microscope fitted with a drawing tube, at magnifications of 400× or 600× as indicated in the figure legends. Specimens were deposited either in the collections of the National Museum of Natural History, Smithsonian Institution (USNM) or in the collection of BHK.

List of Species and Localities

Mesocyclops ogunnus Onabamiro, 1957

Thong Khan Kham, Vientiane, Laos, eutrophic pond about 20 yr old, 10 m diameter, heavy microalgae, excrement, no vegetation, 17°59′N 102°38′E, 22 May 1990, col. BHK.

Mesocyclops cf. *pehpeiensis* Hu, 1943
Mesocyclops guangxiensis, new species

Akat, Vientiane, Laos, muddy pond, 10 m diameter, with floating water weeds, 22 May 1990, col. BHK.

Mesocyclops cf. *pehpeiensis*

Institute of Malaria and Parasitic Diseases (IMPD), Chanthabouri, Vientiane, Laos, drain, water clear, heavy emergent and some floating water weeds, muddy bottom with some blue-green algae, 24 May 1990, col. BHK.

Mesocyclops cf. *pehpeiensis*
Mesocyclops thermocyclopoides acutus
Dussart & Fernando, 1988

Sisavath, Vientiane, Laos, polluted pond in back garden, 5 m diameter, water grey, marginal vegetation, 1 Jun 1990, col. BHK.

Mesocyclops guangxiensis

That Luang Village, Vientiane, Laos, eutrophic pond in back garden, 10 × 5 m, much green algae, emergent and floating vegetation, 2 Jun 1990, col. BHK.

Mesocyclops cf. *thermocyclopoides* of
Lim & Fernando, 1985

Restored Sword Lake, Hanoi, Viet Nam, 21°01′N, 105°52′E, polluted lake, about 50 ha, heavy green microalgal bloom, concrete sides, no vegetation, 13 Jun 1989, col. BHK.

Mesocyclops guangxiensis

Domestic water storage tanks 1 and 2, Hanoi, Viet Nam, 1 Nov 1990, col. Vu Sinh Nam.

Mesocyclops guangxiensis

Nanning, Guangxi Province, China, 22°50′N 108°19′E, col. Wu Neng and Lin Jie-yan; from colony at QIMR, 25 Jun 1990.

Taxonomic Account

Family Cyclopidae Burmeister, 1834
Genus *Mesocyclops* G. O. Sars, 1914
Mesocyclops guangxiensis, new species
Figs. 1–3

Mesocyclops guangxiensis (*Gui*).—Lin et al., 1990:262, 263.
Mesocyclops sp.—Lin et al., 1990:259.

Material.—Holotype ♀, dissected in PVL on slide, USNM 251621; paratypes, ♀, dissected in PVL on slide, and 9 ♀♀, 8 copepodids, USNM 251622; all from culture at QIMR, collected from Nanning, province of Guangxi, China, by Wu Neng and Lin Jie-yan, preserved 25 Jun 1990.

Non-paratype material.—2 ♀♀, Akat, Vientiane, Laos, 22 May 1990, USNM 251623. 1 ♀, dissected on slide in glycerin jelly, and 1 ♀, 2 ♂♂, Sisavath, Vientiane, Laos, 1 Jun 1990, USNM 251624. 1 ♀, dissected on slide in PVL, 1 ♀, mounted whole on slide in glycerin jelly, and 11 ♀♀, 3 ♂♂, 18 copepodids, That Luang Village, Vientiane, Laos, 2 Jun 1990, USNM 251625. 3 ♀♀, 1 ♂, 6 copepodids, Domestic Water Storage Tank No. 1, Hanoi, Viet Nam, 1 Nov 1990, collected by Vu Sinh Nam, USNM 251626. 20+ adults and copepodids, Domestic Water Storage Tank No. 2, Hanoi, Viet Nam, 1 Nov 1990, collected by Vu Sinh Nam, USNM 251627. Unmounted specimens ethanol-preserved. Additional, non-paratype material in collection of BHK.

Female.—Morphology similar to that of *Mesocyclops leuckarti* (Claus, 1857) as redescribed by Van De Velde (1984) except as noted in following description.

Length of holotype, excluding caudal setae 1080 μm; range of lengths of paratype females, 1060–1240 μm (median = 1130 μm; $n = 11$). Pedigers 3 and 4 with scattered shallow round pits on lateral surfaces. Pediger 5 (Fig. 1a, b) haired laterally, ventralmost hairs slightly thicker than more dorsal hairs and arranged in anteroposterior row, more dorsal hairs scattered in poorly defined groups; middle half of dorsal surface of pediger 5 with only 2 hairs near midline common to all congeners. Genital segment (Fig. 1b) longer than broad, posterior ⅔ with shallow pitting on dorsal and ventral surfaces, partly indicated in figure; dorsal surface hairless; segment otherwise ornamented only with group of few tiny spines on lateral surface posterior to leg 6 plate (Fig. 1c, indicated by arrow). Seminal receptacle, anterior expansion concave medially, lateral arms short, rounded, only slightly recurved posteriorly, pore-canal curved. Succeeding 2 urosomites with few scattered pits

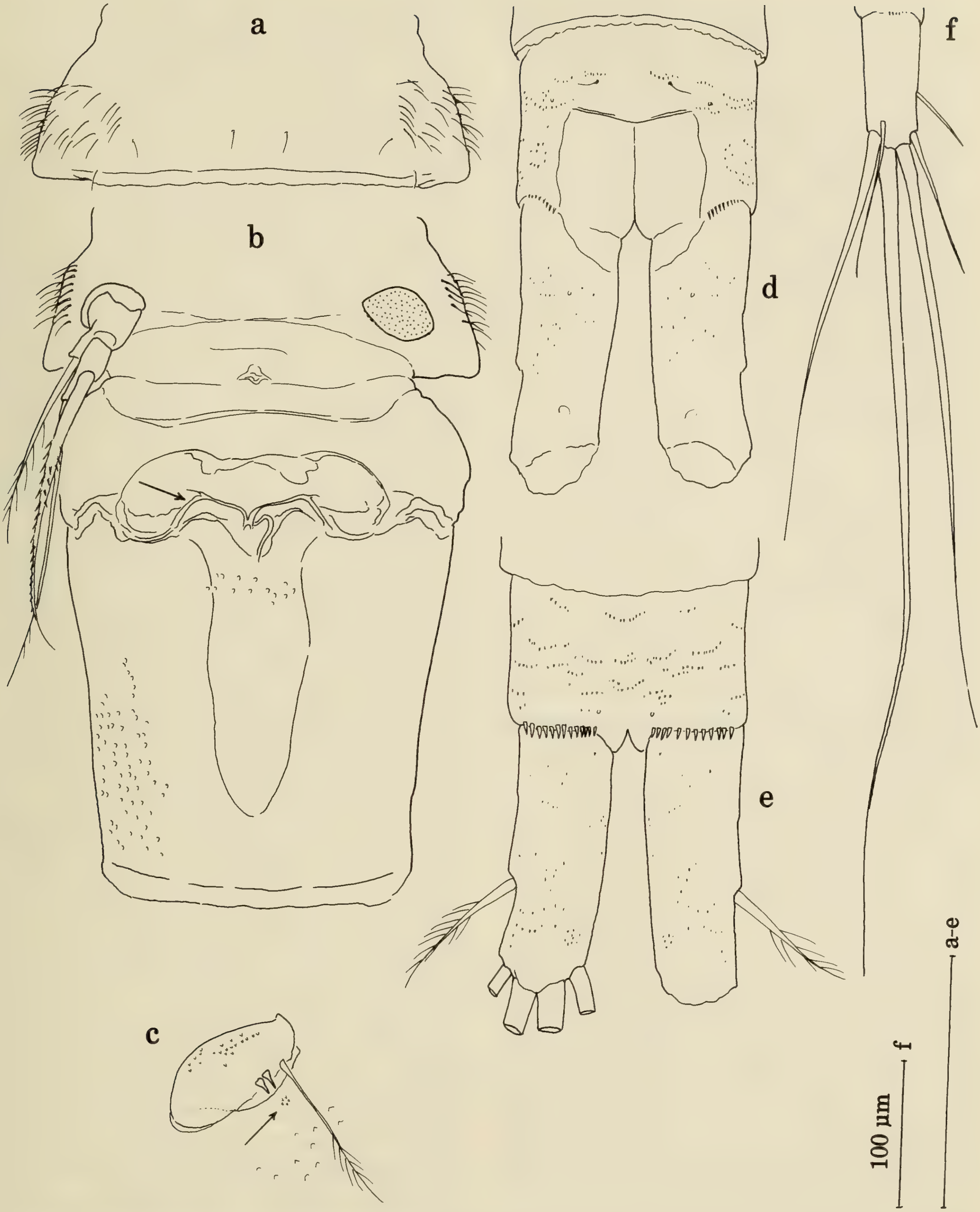

Fig. 1. *Mesocyclops guangxiensis,* new species, female, holotype, USNM 251621. a, Pediger 5, dorsal; b, Pediger 5 and genital segment, ventral (arrow indicates lateral canal of seminal receptacle); c, Leg 6 and adjacent surface of genital segment, left lateral (arrow indicates group of tiny spines posterior to leg 6 plate); d, Anal somite and caudal rami, dorsal, caudal setae omitted; e, Anal somite and caudal rami, ventral, most caudal setae omitted; f, Caudal ramus and caudal setae, right dorsal. Fig. 1a–e drawn at 600× in lactic acid, Fig. 1f drawn at 400× in PVL.

on lateral surfaces. Posterior margin of anal somite (Fig. 1d, e) with small spines dorsally and large spines ventrally, naked laterally. Caudal ramus (Fig. 1d–f) about 2.8 times longer than broad, medial surface of ramus without hairs, no spines at bases of lateral and lateralmost terminal caudal setae. Most caudal setae homonomously plumed, except dorsal seta naked. Lengths of caudal setae of holotype in μm: lateral 50, dorsal 95, medialmost to lateralmost terminal 272, 540, 360, 92. Lateralmost terminal seta about 1.1 times length of caudal ramus.

Antennule (Fig. 2a, b) with irregular rows of small spines on ventral side of articles 1, 4, 5, and 7–13, spine row on article 1 terminating in group of spines; surface of articles 1–4 with few transverse rows of round pits (not shown in Fig. 2a). Membrane of antennule article 16 narrow, finely serrate; membrane of article 17 more coarsely serrate, with deep notch. Antenna article 1 (Fig. 2c, d), in addition to basic spine pattern of *Mesocyclops* species (Fiers & Van De Velde 1984, Van De Velde 1984; normally present groups of spines numbered 1 in Fig. 2c, d), with several irregular rows (rather than usual 1 row of congeners) of minute spines on medial part of caudal side (numbered 2 in Fig. 2c), numerous irregularly scattered minute spines on distal ⅓ of caudal side (numbered 3 in Fig. 2c), and 3 transverse rows (rather than usual 1 row) of minute spines near proximal margin of frontal side (numbered 4 in Fig. 2d). Mandible (Fig. 2e) with 3 groups of small, tiny, and minute spines near palp. Maxillule (Fig. 2f), palp without spines on surface of basis, 2 distal setae of basis and 3 setae of endopodite with tiny short setules. Maxilla (Fig. 2g), article 2 (coxa) with irregular row of distally directed spines on frontal side, ventral surface of same article slightly rugose proximally and pitted distally; suture between articles 1 and 2 not visible on frontal side, complete on caudal side.

Leg 1 (not figured), medial expansion of basipodite not bearing spine. Couplers of legs 1–4 lacking surface ornament; coupler of leg 4 (Fig. 2h) with 2 small obtuse subtriangular prominences on distal margin. Leg 4 coxopodite with few hairs on lateral surface, 2 irregular groups of spines of different sizes on posterior surface, and divided row of large spines on middle of posterodistal margin, usually with 3 or 4 spines in lateral part of row and 4 or 5 spines in medial part. Leg 4 basipodite with proximal row of stiff heavy hairs and distal group of finer hairs on posterior surface of medial expansion. Leg 4 endopodite article 3 (Fig. 2i) with few (3 on left side and 4 on right in holotype) spinules on lateral margin of medial terminal spine; this spine slightly longer than lateral terminal spine.

Leg 5 (Fig. 1b) with seta of article 1 shorter than spine and seta of article 2; spine of article 2 reaching past midlength of genital segment; spine of article 2 slightly longer than seta of article 2 in some specimens. Leg 6 (Fig. 1c) consisting of ovoid plate ornamented with small spines on anterior half and bearing dorsal plumed seta and 2 short spines on posterodorsal border.

Variation.—The lateral canals of the seminal receptacle [termed posterior margins of the seminal receptacle by Van De Velde (1984); indicated by arrow in Fig. 1b] are more or less slightly fused anterior to the copulatory pore in different specimens from the type population. In the other populations examined, these canals are slightly fused near the pore (Fig. 3a). In some specimens from the type population, the lateral arms of the seminal receptacle are slightly concave on the anterolateral ⅓, similar to *M. thermocyclopoides* s. s. [Kiefer 1981: fig. 2(3)]. The extent of the shallow pitting on the posterior prosomites, the genital segment, and the posterior urosomites varies in different specimens.

Two of a total of 14 females from That Luang, Laos have 3–4 spines at the base of the lateralmost terminal caudal seta. In some

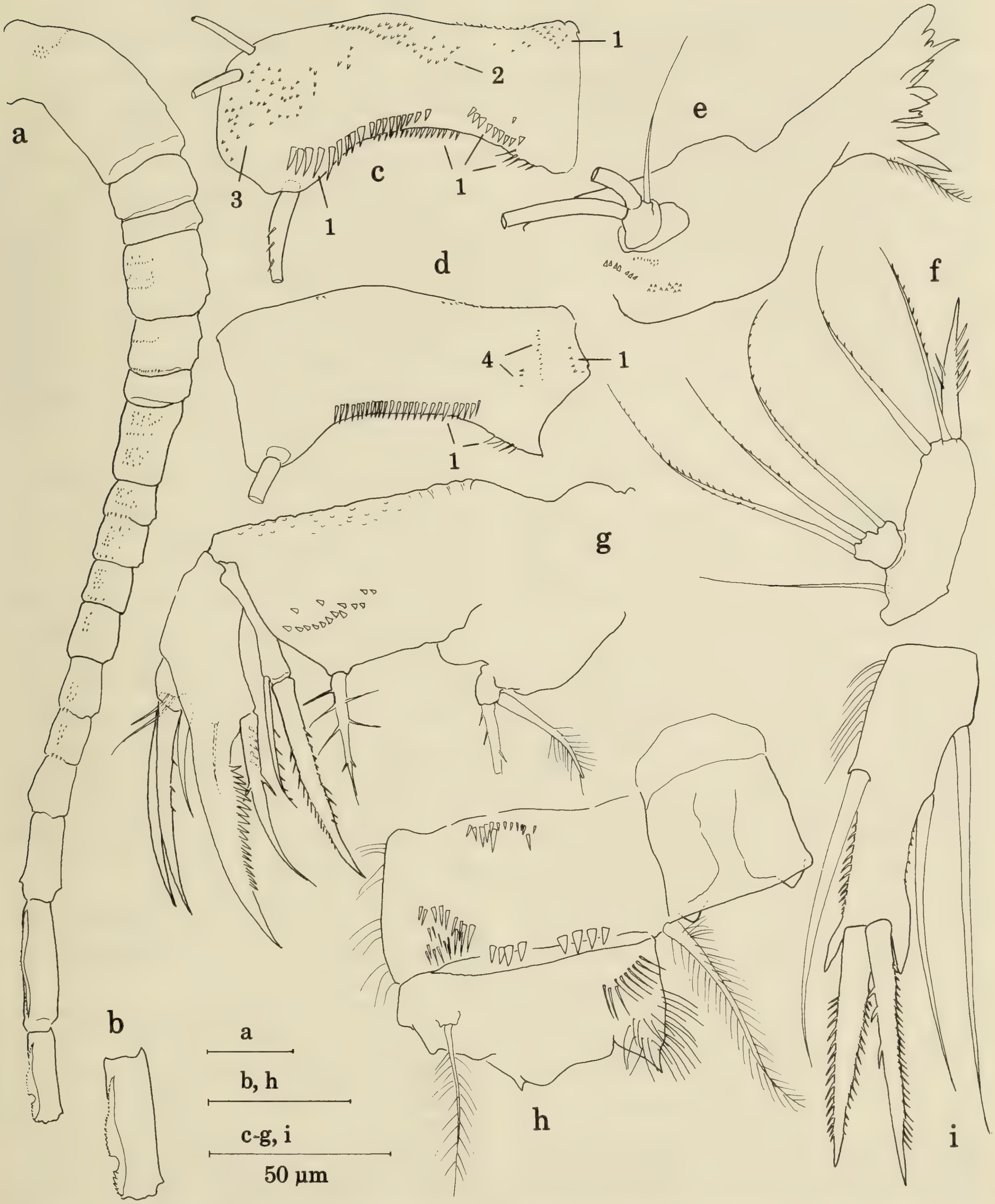

Fig. 2. *Mesocyclops guangxiensis,* new species, female, holotype, USNM 251621. a, Antennule (setae omitted), ventral side; b, Antennule article 17; c, Antenna article 1 (basipodite), caudal side (numbers indicate groups of spines; see text); d, Antenna article 1 (basipodite), frontal side (numbers indicate groups of spines); e, Mandible; f, Maxillular palp; g, Maxilla, frontal side; h, Leg 4 coupler, left coxopodite and basipodite, posterior; i, Left leg 4 endopodite 3, posterior. Fig. 2a, b drawn at 400× and Fig. 2c, d at 600× in lactic acid; Fig. 2e–i drawn at 600× in PVL.

females from this population, the lateral arms of the seminal receptacle are slightly more recurved (Fig. 3a), and the caudal side of the antenna article 1 (Fig. 3b) bears fewer tiny spinules while retaining a similar general pattern. In females from Sisavath and That Luang the prominences on the distal margin of the leg 4 coupler (Fig. 3c) are acute. The leg 4 endopodite 3 medial terminal spines have 0–6 spinules on the lateral margin in the populations examined; females from Hanoi Water Tank No. 2 tend to have the fewest spinules at this location.

Male.—No males from the type population were available.

Type locality.—Nanning, Guangxi Province, China.

Etymology.—Named for the province of China in which the type locality is located. This is one of two species appellations provisionally suggested by Lin et al. (1990), the second suggestion being *Gui.*

Comparisons.—Presently about 21 taxa of the genus *Mesocyclops* are known that lack a spine on the leg 1 basipodite medial expansion, and also have hairs on the lateral surface of the pediger 5. Of these, *M. aspericornis* (Daday, 1906), *M. microlasius* Kiefer, 1981, *M. pilosus* (Kiefer, 1930), and *M. spinosus* Van De Velde, 1984 are most easily distinguished from *M. guangxiensis* by having hairs along all or part of the medial surface of the caudal ramus. In *M. major* G. O. Sars, 1927 and *M. insulensis* Dussart, 1982, among other differences, the prominences on the leg 4 couplers are more elongate and acute, the leg 4 coupler has a row of fine hairs on its posterior surface, and the leg 4 endopodite 3 medial terminal spines are spinulate along most of the lateral margins. Similarly spinulate lateral margins of the leg 4 endopodite 3 medial terminal spines separate these species from *M. guangxiensis*: *M. thermocyclopoides australiensis* (G. O. Sars, 1908), *M. dussarti* Van De Velde, 1984, *M. granulatus* Dussart & Fernando, 1988, *M. isabellae* Dussart & Fernando, 1988, *M. isabellae* var. *nepalensis* Dussart & Fernando, 1988, *M. ogunnus* Onabamiro, 1957, *M. thermocyclopoides* s. l. of Collado et al. (1984), and *M. woutersi* Van De Velde, 1987. *Mesocyclops aequatorialis* (Kiefer, 1929) and *M. aequatorialis similis* Van De Velde, 1984 both have the pore-canal of the seminal receptacle straight, not curved, and small spines at the bases of both the lateral seta and the lateralmost terminal caudal seta. *Mesocyclops notius* Kiefer, 1981 has spines at the bases of both the lateral and lateralmost terminal caudal setae (confirmed by Dussart & Fernando 1988), as does *M. affinis* Van De Velde, 1987. *Mesocyclops thermocyclopoides* s. s. Harada, 1931 as redescribed from the type locality in Taiwan by Kiefer (1981) and Van De Velde (1987) has only a single, distal group of fine hairs on the leg 4 basipodite medial expansion, and the laterad parts of the anterior margins of the lateral arms of the seminal receptacle are concave rather than convex. *Mesocyclops thermocyclopoides acutus* Dussart & Fernando, 1988 has spines at the base of the lateralmost terminal caudal seta, and the pore-canal of the seminal receptacle is straight. The foregoing four species also differ from *M. guangxiensis* in the antenna spine pattern, chiefly in having a distal row or group of large spines, in addition to small distal spines on the caudal side. This antenna spine pattern with a group of large distal spines was reported for another very similar taxon, *M.* cf. *thermocyclopoides* by Lim & Fernando (1985).

Mesocyclops guangxiensis is a member of the *thermocyclopoides*-complex, which is primarily a paleotropical group except for *M. thermocyclopoides* s. l. of Collado et al. (1984) from Costa Rica. Taxonomic understanding of this complex is as yet unsatisfactory; some previous confusions were discussed by Van De Velde (1984, 1987), Lim & Fernando (1985), and Dussart & Fernando (1988).

All these authors agree that scrutiny of all possible microcharacters is necessary for adequate species discrimination. *Mesocyclops guangxiensis* presents several microcharacters which have not been described

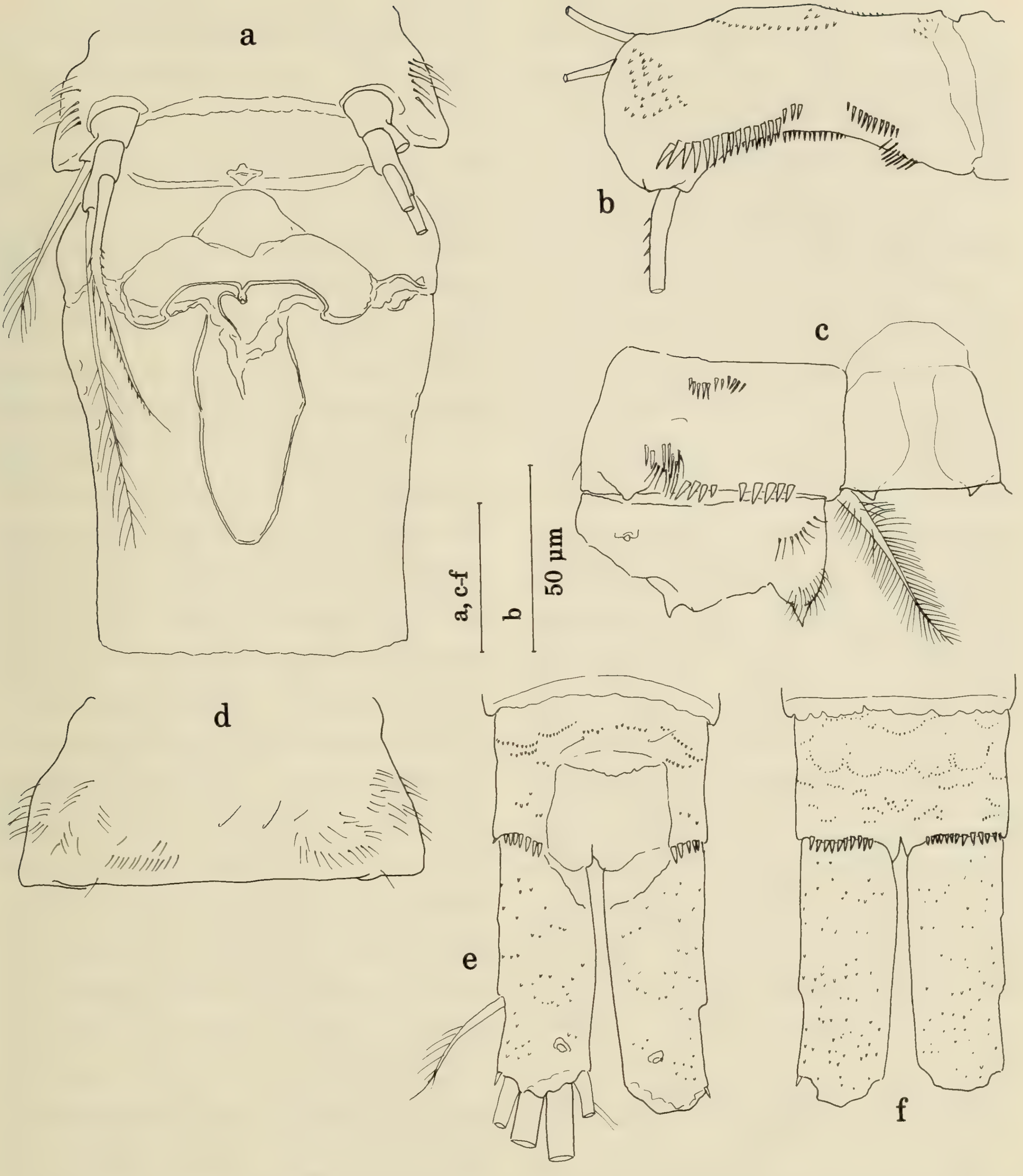

Fig. 3. a–c, *Mesocyclops guangxiensis,* new species, dissected female from That Luang Village, Laos, USNM 251625. a, Pediger 5 and genital segment, ventral; b, Antenna article 1 (basipodite), caudal side; c, Leg 4 coupler, left coxopodite and basipodite, posterior. d–f, *Mesocyclops ogunnus* Onabamiro, 1957, female from Thong Khan Kham, Laos, USNM 251628. d, Pediger 5, dorsal; e, Anal somite and caudal rami, dorsal, most setae not indicated; f, Anal somite and caudal rami, ventral, setae omitted. Figs. drawn at 600×; Fig. 3a, d–f drawn in lactic acid, Fig. 3b, c in PVL.

for all known members of the complex, nor indeed for most congeners. A similar pattern of antennular spines, especially the group rather than the single row of spines on article 1 has only been described for *M. ogunnus,* in which it is apparently a variable character (Nigerian population, Van De Velde 1984). The three groups of mandibular spines are very characteristic for *M. guangxiensis.* Van De Velde (1984) showed the mandibles of *M. leuckarti* and *M. ogunnus* each with only one group of spines. The setae of the maxillular palp were shown as naked in all species illustrated by Van De Velde (1984), but this may have been an intentional simplification. Van De Velde (1984) noted a row of small spines on the frontal side of the maxilla of only one, *M. ogunnus,* of the several African species which she examined. Since the ornament of the leg 4 coxopodite and basipodite has been figured only partly in the case of most species, it is impossible to evaluate the taxonomic utility of this ornament at the present time. The interrupted row of few, very large spines on the posterodistal margin of the coxopodite of *M. guangxiensis* seems to be unusual in the genus. As Van De Velde (1984) noted, the exact nature of the ornament of the medial expansion of the leg 4 basipodite is a species-specific character. This ornament has been indicated only vaguely by most authors. Spines on the surface of the leg 6 plate have not been noted previously in a species of *Mesocyclops,* although Van De Velde (1984) and others have indicated the presence of one or more groups of spines and/or pores on the genital segment posterior to the leg 6 plate in several species. Inter- and intrapopulational variation in these characters has not yet been examined satisfactorily in any species of *Mesocyclops.*

Mesocyclops ogunnus Onabamiro, 1957
Fig. 3d–f

Material.—2 ♀♀, each dissected on slide in PVL, and 34 ♀♀, 23 copepodids, alcohol-preserved; all from Thong Khan Kham, Vientiane, Laos, 22 May 1990, USNM 251628. Additional specimens in collection of BHK.

Female.—Range of lengths 1040–1212 μm (median = 1120 μm; $n = 10$). Differing in only a few respects from redescription of *M. ogunnus* by Van De Velde (1984). Pediger 5 (Fig. 3d) of Laotian specimens somewhat hairier dorsally, although basic pattern of rows of hairs approaching dorsal midline similar. Anal somite (Fig. 3e, f) more thickly set with rows of tiny spines in Laotian specimens. Lateral caudal seta (Fig. 3e, f) lacking spines at base. Maxilla article 2 (coxa) with tiny spines scattered over distal half of frontal side in addition to row of tiny spines as figured on this segment by Van De Velde (1984). Leg 4 coupler processes broadly triangular, acute.

Comparisons.—The Laotian specimens possess a row of spines on the mandibular palp. Only two species are known to have such a spine row, *M. ogunnus* and *M. salinus* Onabamiro, 1957 (as redescribed by Van De Velde 1984). *Mesocyclops salinus,* so far known only from subsaharan Africa, has the pediger 5 naked and the leg 4 coupler haired, and in several other respects does not resemble the Laotian specimens. *Mesocyclops ogunnus* was redescribed from subsaharan Africa and Israel by Van De Velde (1984), and has since been reported from Indonesia (Dussart & Sarnita 1987) and Bangladesh (Dussart & Fernando 1988). The Laotian specimens match or fall within the range of variation of the African material of *M. ogunnus* in all major characters. The hairier pediger 5, and the different maxilla and anal somite spine patterns of the Laotian material are probably not significant at the species level. Van De Velde (1984) noted interpopulational variations in several characters of *M. ogunnus,* but not in the shape of the leg 4 coupler processes, which she figured as small and rounded; however Dussart & Fernando (1988) drew these processes as more developed and acute in specimens from Bangladesh. The lateral caudal setae of *M. ogunnus* have spines at their bases in African populations, while the Laotian specimens do not. These variations from the African populations might be considered to have taxonomic significance if associated with other morphological differences, but in view of the overall similarity of the Laotian specimens with existing descriptions of *M. ogunnus,* referral to this species seems justifiable.

Mesocyclops cf. *pehpeiensis* (Hu, 1943)

Material.—70+ ♀♀, 3 ♂♂, 50+ copepodids, Akat, Vientiane, Laos, 22 May 1990, USNM 251629. 1 ♀, dissected on slide in PVL, and 7 ♀♀, IMPD drain, Vientiane, Laos, 24 May 1990, USNM 251630. 14 ♀♀, Sisavath, Vientiane, Laos, 1 Jun 1990, USNM 251631. Unmounted specimens ethanol-preserved. Additional material in collection of BHK.

Comparisons.—These specimens match the original description of *M. Leuckarti pehpeiensis* by Hu (1943), from Szechuan, and later descriptions by Tai & Chen (1979) from many localities in central China and by Kim & Chang (1989) from Korea. The single exception is that the lateral margin of the leg 4 endopodite 3 medial terminal spine of the several Laotian specimens examined has very few spinules, and the original as well as subsequent descriptions from China and Korea all show spinules along most of the margin of this spine.

Lim & Fernando (1985) provided figures of a species from Malaysia that they referred to *M. pehpeiensis*; their figure shows the leg 4 endopodite 3 medial terminal spine with few lateral marginal spinules. The same species was recorded from Burma, Malaysia, Sri Lanka and probably northern Australia by Dussart & Fernando (1985a) and again from Sri Lanka (Dussart & Fernando 1985b). These authors provided some figures (Dussart & Fernando 1988), which are congruent with the material from Laos.

Unfortunately, existing descriptions of Chinese specimens are so incomplete that it is impossible reliably to identify any species as *M. pehpeiensis* without topotype material for comparison. For this reason we have identified the specimens from Laos as this taxon only provisionally.

Mesocyclops cf. *thermocyclopoides* of Lim & Fernando, 1985

Mesocyclops cf. *thermocyclopoides* Harada, 1931.—Lim & Fernando, 1985:73, 80–83, figs. 46–50, tab. 3.—Dussart & Fernando, 1985b:230, 246, 247, 248, figs. 96–99.—Van De Velde, 1987:156.

?Non *M. dussarti* Van De Velde, 1984.—Dussart & Fernando, 1988:248.

Material.—1 ♀, dissected on slide in glycerin jelly, 1 ♀, dissected on slide in PVL, and 1000+ adults and copepodids, alcohol-preserved, Restored Sword Lake, Hanoi, Viet Nam, 13 Jun 1989, USNM 251632. Additional material in collection of BHK.

Comparisons.—Lim & Fernando (1985) provided partial figures of a species from several localities in Malaysia, which they called "cf. *thermocyclopoides.*" Dussart & Fernando (1985b) provided amplified figures and discussion of this species, still calling it "cf. *thermocyclopoides,*" and gave the distribution as extending from Singapore to India. Van De Velde (1987) reproduced Kiefer's figures of topotype specimens of *M. thermocyclopoides* Harada s. s., and suggested that Lim and Fernando's species might refer to *M. thermocyclpoides* s. s.

The specimens from Hanoi resemble these three sets of figures, although each set is incomplete and not in total agreement. In particular, the seminal receptacles and spine patterns of the antenna are very similar.

Dussart & Fernando (1988) later asserted that *M.* cf. *thermocyclopoides* of Lim & Fernando (1985) is a synonym of *M. dussarti* Van De Velde, 1984, from Mali. However, if the Hanoi species is the same that Lim & Fernando (1985) and Dussart & Fernando (1985b) had from Asia, which seems probable, then the Hanoi material differs from Van De Velde's (1984) original description of *M. dussarti* in several respects. Pediger 5 and the genital segment of *M. dussarti* are covered with hairs dorsally, but in the Hanoi specimens the pediger 5 is haired only laterally and the genital segment is not

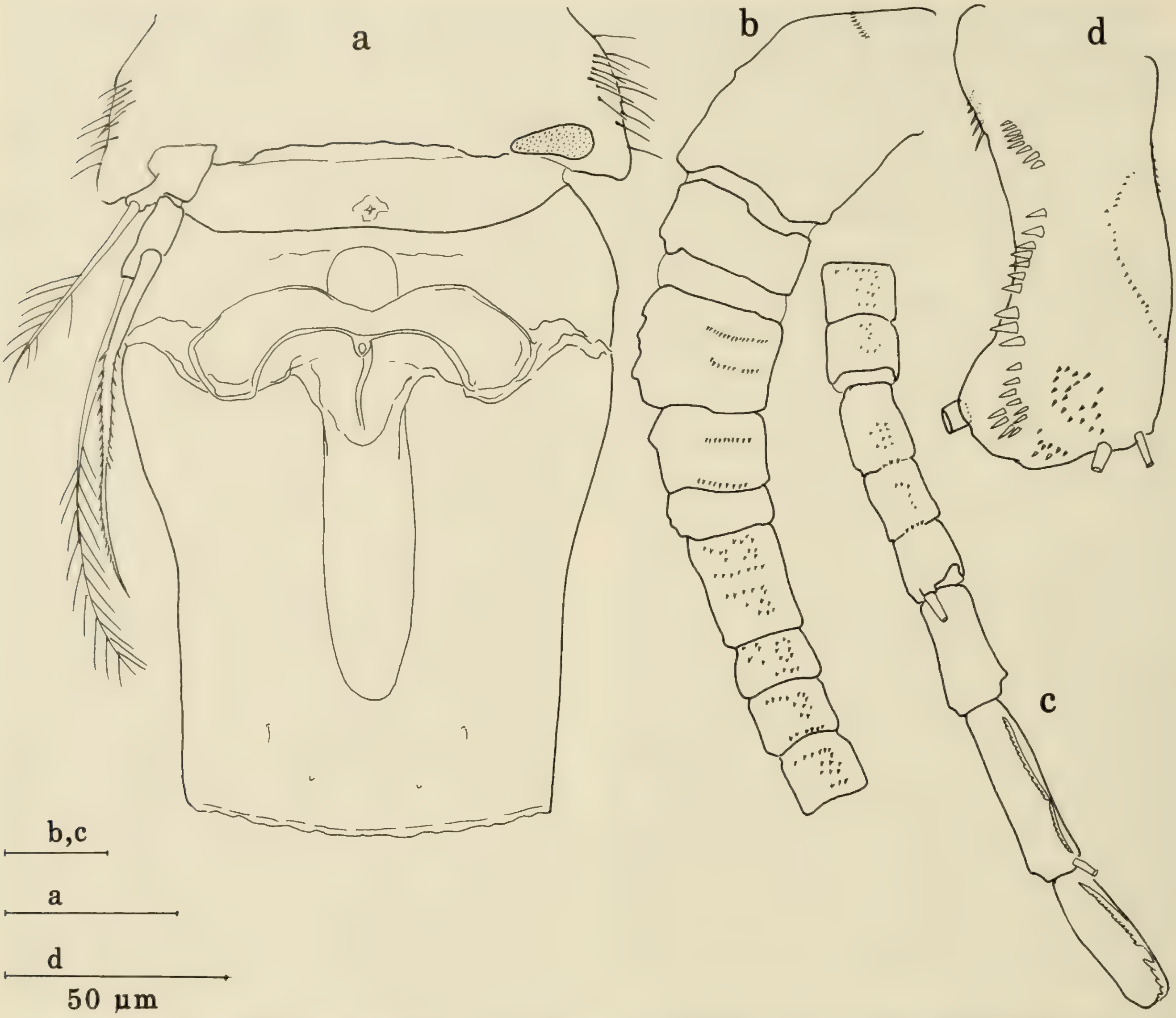

Fig. 4. *Mesocyclops thermocyclopoides acutus* Dussart & Fernando, 1988, dissected female from Sisavath, Vientiane, Laos, collection of BHK. a, Pediger 5 and genital segment, ventral; b, Antennule articles 1–9 (setae omitted), ventral side; c, Antennule articles 10–17 (most setae omitted), ventral side; d, Antenna article 1 (basipodite), caudal side. Fig. 4a, d drawn at 600×, Fig. 4b, c at 400×; Fig. 4a–c drawn in lactic acid, Fig. 4d in PVL.

haired. In *M. dussarti,* the lateralmost terminal caudal seta has spines at its base; such spines are lacking in the Hanoi specimens. In *M. dussarti,* the medial terminal spine of leg 4 endopodite 3 is distinctly shorter than the lateral terminal spine; these spines are subequal in the Hanoi specimens. Several features of existing descriptions of Asian populations, such as the lack of spines at the bases of the lateral and lateralmost terminal caudal setae of females from Sri Lanka figured by Dussart & Fernando (1985b), agree better with the Hanoi specimens than with *M. dussarti.*

In view of these differences and the incompleteness of the published information on the several Asian populations, it seems better to maintain *M.* cf. *thermocyclopoides* of Lim & Fernando as a separate taxon, until the range of variation in all morphological characters can be assessed.

Mesocyclops thermocyclopoides acutus
Dussart & Fernando, 1988
Fig. 4

Mesocyclops thermocyclopoides acutus Dussart & Fernando, 1988:254, 255, figs. 43–50.

Material.—1 ♀, ethanol-preserved, USNM

251633, and 1 ♀, dissected in PVL, collection of BHK, pond, Sisavath, Vientiane, Laos.

Description and comparisons.—Lengths of 2 females, 1150 μm and 1280 μm. Two specimens from Laos matching original description by Dussart & Fernando (1988), in all particulars including shape of seminal receptacle (Fig. 4a), with pore-canal nearly straight; single deep, quadrate notch of serrate hyaline membrane of antennule (Fig. 4c); and pattern of spines on caudal side of antenna (Fig. 4d). Antennule (Fig. 4b, c) additionally with 2 transverse rows of small spines on articles 3 and 4 and groups of spines on articles 6–13. Mandible with 1 group of spines proximal to palp. Maxilla with row of spines on frontal side of coxa, similar to that of *M. guangxiensis* (Fig. 2g).

Discussion.—Assignment of the specimens from Laos to *M. thermocyclopoides acutus* is based on their close correspondence with the detailed description by Dussart & Fernando (1988). The present record from Laos represents a considerable range extension for this subspecies, since the original description was of specimens from West Kalimantan, Indonesia.

Acknowledgments

We thank Mrs. Cheng-su Houchins, who kindly translated some locality records from Tai & Chen (1979). Several colleagues assisted with collections, namely Prof. Wu Neng and Mr. Lin Jie-yan, Guangxi Institute of Parasitic Diseases Control, Nanning; Dr. Vu Sinh Nam, Institute of Epidemiology and Microbiology, Hanoi; and Dr. Bounlay Phommasack, *Aedes* Control Unit, Vientiane. The collections of BHK were facilitated by Dr. L. Self, World Health Organization, Manila. Suggestions by three reviewers resulted in improvements in the text.

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A COLLECTION OF THALASSINIDEA (CRUSTACEA: DECAPODA) FROM THE PACIFIC COAST OF COLOMBIA, WITH DESCRIPTION OF A NEW SPECIES AND A CHECKLIST OF EASTERN PACIFIC SPECIES

Rafael Lemaitre and Gabriel E. Ramos

Abstract.—Twelve species of Thalassinidea are reported from the Pacific coast of Colombia, bringing to fourteen the total number of thalassinids known from this coast. Of the twelve species reported, one is new, *Neaxius frankeae*; five had not been previously reported for this coast: *Lepidophthalmus bocourti* (A. Milne Edwards), *Callianidea laevicauda* Gill, *Pomatogebia rugosa* (Lockington), *Upogebia maccraryae* Williams, and *U. tenuipollex* Williams; and one, *Axiopsis serratifrons* (A. Milne Edwards), was unknown in the eastern Pacific. A checklist of all known species of Thalassinidea from the eastern Pacific is included.

As a result of sampling efforts during the past 10 years by several biologists along the poorly explored Pacific coast of Colombia, an important collection of thalassinid shrimps was obtained. The material is of considerable value because the thalassinids from this coast have not been adequately sampled, and because many of the species in this group are incompletely known, some based only on a few specimens. The material contains 12 species, including a new species, *Neaxius frankeae.* Five species, *Lepidophthalmus bocourti* (A. Milne Edwards, 1870), *Callianidea laevicauda* Gill, 1859, *Pomatogebia rugosa* (Lockington, 1878), *Upogebia maccraryae* Williams, 1986, and *U. tenuipollex* Williams, 1986, are reported for the first time from this coast. One of our specimens has been found to represent *Neocallichirus grandimana* (Gibbes, 1850), a species that also occurs in the western Atlantic. Also discovered in the collection is a juvenile specimen of *Axiopsis serratifrons* (A. Milne Edwards, 1873), a morphologically variable species that is broadly distributed in the tropics but was previously unknown from the eastern Pacific. One species of *Pomatogebia* Williams & Ngoc-Ho, 1990, and four of *Upogebia* Leach, 1814, are present in the material. Finally, one specimen could only be assigned to an undetermined species of the genus *Axianassa* Schmitt, 1924, due to its poor condition. Except for the species of *Pomatogebia* and *Upogebia,* discussed by Williams (1986) and Williams & Ngoc-Ho (1990), and *Callianidea laevicauda,* discussed by Kensley & Heard (1991), the species are illustrated, and the most important recognition characters, coloration in life, and habitat where the specimens were collected, are included. In addition, a checklist of all known Thalassinidea from the eastern Pacific is presented (see Appendix), indicating the most recent nomenclatorial changes. A total of 14 species are now known from the Pacific coast of Colombia.

The specimens used are deposited at the "Colección de Referencia de la Sección de Biología Marina, Universidad del Valle" (CRBMUV), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The abbreviation "CL" indicates the carapace length measured along the dorsal midline, from the tip of the rostrum to the posterior margin.

Systematics

Family Axiidae Huxley, 1878

Neaxius frankeae, new species

Fig. 1

Material examined.—La Barra, Gorgona Island: ♂ holotype, USNM 251731, CL 7.2 mm, 1 Feb 1987, coll.: R. Franke. (parts missing from holotype: antennal flagella, left antennular flagella, left cheliped, and all pereopods except right 1st and 5th).

Description of holotype.—Rostrum triangular, exceeding eyes, reaching to about distal margin of second antennular segment, bifurcated at tip into strong upwardly curved spines; lateral margins each with 2 strong spines directed obliquely upward and forward, and extending posteriorly as ridge with 2 small spines near base of rostrum; dorsal surface with median ridge bearing 3 small blunt spines, and row of tufts of plumose setae near lateral margin. Carapace smooth, anterior margin with strong antennal spine and 3 small subantennal spines. Branchiostegite with anterior margin rounded. Cephalic groove weakly marked ventrolaterally, unarmed.

Corneae well developed, dilated, pigmented; distal margin reaching to about base of bifurcated spines of rostrum.

Antennular peduncles reaching to about distal ¼ of fourth antennal segment; segments each with transverse row of setae on distal margin.

Antennal peduncle exceeding rostrum by about ½ length of fourth segment; 1st segment unarmed; second segment with small spine proximally on dorsal surface, and with strong spinelike dorsodistal projection reaching slightly beyond tip of rostrum; acicle extending slightly beyond tip of dorsodistal projection of second segment, terminating in strong spine, and with 2 strong spines on ventral margin; third segment with ventral spine; fourth and fifth segments slender, unarmed.

Epistome armed medially with small spine between first segments of antennules, and 2 inwardly curved spines on lateral angle.

Third maxilliped slender, with exopod and long setae on ventral margin of segments; coxa with small spine mesially; basis with small spine ventrally; ischium with well developed crista dentata formed by 12 sharp to blunt teeth and strong distal tooth directed mesiad; merus armed with 4 strong spines (increasing in length distally) on ventrolateral margin, and small dorsodistal spine; carpus with 2 (right) and 3 (left) spines on ventrolateral margin; propodus and dactyl unarmed.

Right cheliped (pereopod 1) with setae on dorsal and ventral margins; fingers with tufts of setae on lateral and mesial face; ischium and merus with row of spines on ventral margin, merus also with dorsal row of spines; carpus with 2 dorsodistal spines and spine on ventrodistal angle. Palm smooth on lateral and mesial surfaces, with row of tufts of setae on lateral face near, and parallel, to proximal margin; dorsal margin with at least 5 small spines (palm damaged on dorsal and part of lateral surfaces); ventral margin unarmed, well delimited. Fixed finger with large blunt tooth pointing obliquely forward at about midlength of cutting edge, and small blunt teeth proximally. Dactyl with cutting edge more or less straight on distal ⅔ and proximally with weakly developed teeth.

Fifth pereopod subchelate; propodus with numerous simple setae on distomesial margin, and 1 serrate seta on distolateral angle; dactyl slender, minutely serrated on flexor margin (visible under high magnification).

Coxa of pereopods 1–4 with 2–4 spines on mesial face; coxa of pereopod 5 unarmed. Epipods present on 3rd maxilliped and pereopods 1–4. Sternite of pereopod 4 divided into 2 processes separated by deep groove; each process with spine directed anteriorly. Sternite of pereopod 5 with lateral

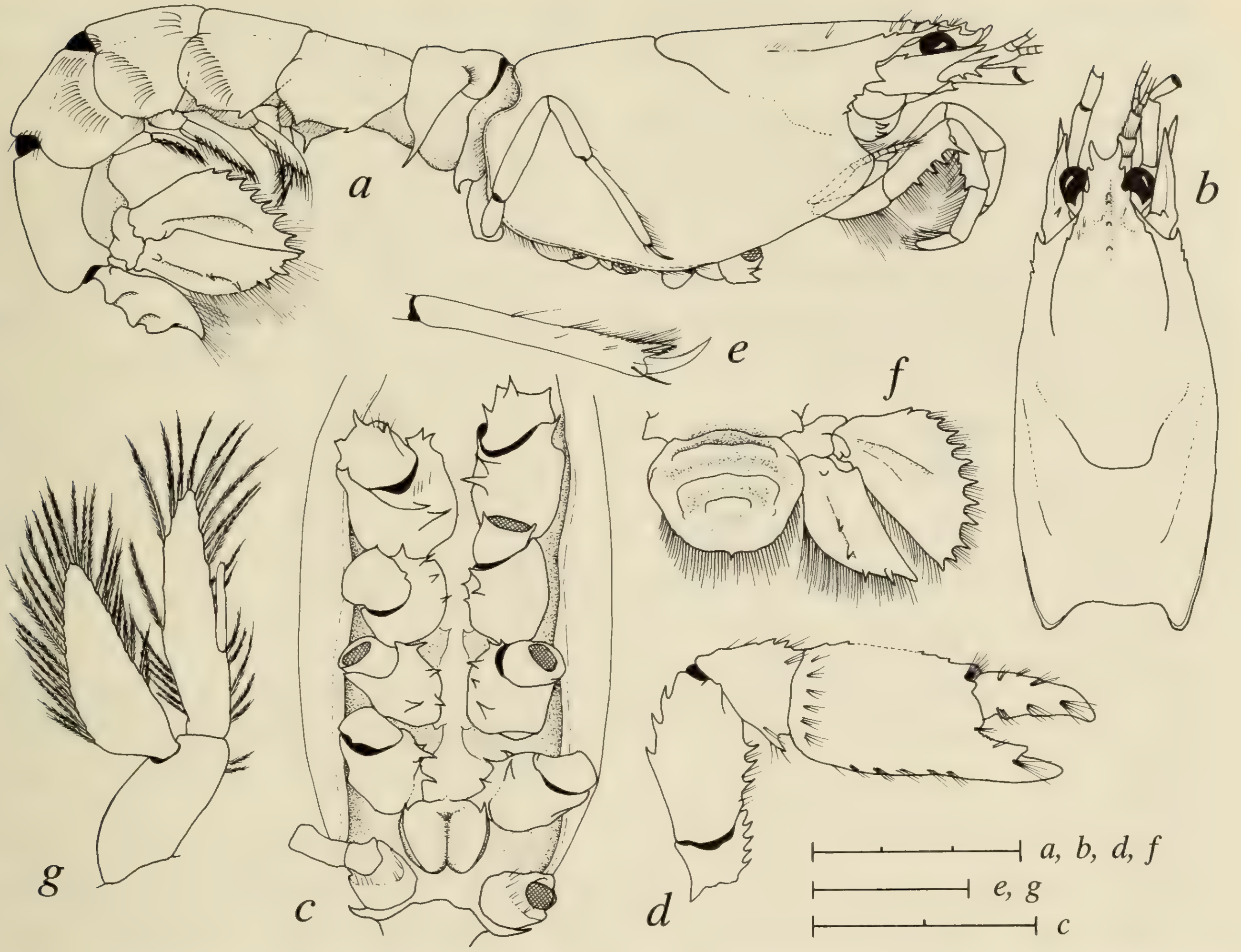

Fig. 1. *Neaxius frankeae,* new species. Holotype, USNM 251731 a, body, lateral view; b, carapace and cephalic appendages, dorsal view; c, sternum; d, right cheliped, lateral view; e, propodus and dactyl of pereopod 5, lateral view; f, telson and right uropod, dorsal view; g, male right pleopod 2, anterior view. Scales equal 3 mm (a, b, d, f), 1 mm (e, g), 2 mm (c).

projection on each side in form of spine directed ventrally and slightly forward.

Abdomen about 1.6 times as long as carapace. Dorsal surface of somites smooth, with scattered setae. Pleura of somite 1 terminating ventrally in strong spine; pleura of somites 2–4 with 2 small spines on ventral margin, pleura of somites 3–5 with transverse row of setae. Sternite of somite 2 armed with spine medially. Somite 6 about 1.4 times as long as somite 5. Pleopod 1 absent. Pleopods 2–5 each with appendix interna, lacking appendix masculina; exopod and endopod with long plumose setae.

Uropods longer than telson, setose on margins; outer ramus lacking transverse suture, with row of 12 strong spines on outer (posterior) margin, and straight inner margin; inner ramus with straight lateral margin terminating distally in strong spine, with 2 spines near edge of posterior margin, and median longitudinal carina bearing 2 small spines.

Telson widest on anterior third, diminishing in width posteriorly. Lateral and posterior margins with long setae. Dorsal surface with 3 well defined transverse ridges curving posteriorly on lateral margins. Posterior margin with median spine.

Color in life.—Body, chelipeds and walking legs white. Internal organs visible through cephalothorax light brown.

Distribution.—Known only from the holotype collected at Gorgona Island, Colombia.

Etymology.—The species is named for the Colombian biologist Rebeca Franke, in recognition of her collecting efforts at Isla Gorgona.

Habitat.—Near low tide level, in burrows formed by gravel and coralline sand. Found with various species of shrimps of the genus *Alpheus.*

Remarks.—With the description of this new species there are now four in the genus *Neaxius* Borradaile, 1903, formerly a subgenus of *Axius* Leach, 1815, but recently elevated to generic rank by Sakai & De Saint Laurent (1989). The other species are: *N. acanthus* (A. Milne Edwards), from the Indo-Pacific, *N. glyptocercus* (von Martens), from Australia, and *N. vivesi* (Bouvier), from the eastern Pacific.

A comparison of our specimen with the descriptions of *N. acanthus* and *N. glyptocercus* provided by Poore & Griffin [1979: 235, 236, figs. 7, 8; as *Axius* (*Neaxius*) *acanthus* and *A.* (*N.*) *glyptocercus*], and with specimens deposited in the USNM of *N. vivesi,* shows that the new species is most similar to the eastern Pacific *N. vivesi* but clearly differs from it in a number of characters. Although a single specimen of *N. frankeae* is known, it appears that it is a species with individuals of much smaller size than *N. vivesi* (specimens examined of *N. vivesi* all exceeded 25 mm in CL whereas the type of the new species has a CL of only 7.2 mm). In *N. frankeae,* the cervical groove is unarmed whereas in *N. vivesi* the lateral portion is armed with several spines; the second segment of the antennal peduncle bears one spine whereas there are four (two dorsomesial and two dorsolateral) in *N. vivesi*; the antennal acicle is armed with two ventral spines whereas there are five in the USNM material of *N. vivesi,* and four, according to De Man (1925:59), in the type of *N. vivesi*; the lateral face of the merus and carpus of the major cheliped are unarmed whereas in *N. vivesi* the merus has a row of lateroventral spines, and the carpus bears a cluster of strong spines; the pleura of abdominal somite 1 terminates in a simple spine whereas in *N. vivesi* this spine is bifid or trifid; the ventral margin of the pleurae of abdominal somites 2–4 are armed with two spines, whereas in *N. vivesi* the pleura of abdominal somite 2 have eight, and those of abdominal somites 3 and 4 have two.

Axiopsis serratifrons
(A. Milne Edwards, 1873)
Figs. 2, 3

Axiopsis serratifrons.—Kensley, 1981:1253, figs. 1–5.—Manning & Chace, 1990:31, figs. 16, 17.

Material examined.—Antiguo Muelle, Gorgona Island: 1 ♀ (juvenile), CL 13.9 mm, 9 Mar 1989, coll.: R. Franke, USNM 251732.

Distribution.—Eastern Pacific: Gorgona Island (Colombia). Indo-Pacific, including the Red Sea. Western Atlantic: Florida to Belize, including Bermuda. South Atlantic: Ascension Island.

Habitat.—Subtidal near low tide level, in substrate of sand and stones.

Remarks.—The morphology and coloration of the single specimen collected generally agrees with Kensley's (1981) detailed redescription of this species, except for the presence in our specimen of rudimentary first pleopods. This pleopod condition, however, can be attributed to the juvenile (sexually immature) stage of our specimen. The only other species of *Axiopsis* Borradaile, 1903, known from the eastern Pacific is *A. baronai* Squires, 1977. The two species can be differentiated by several characters. The gastric region of the carapace of *A. serratifrons* has more spines than in *A. baronai*; the submedian carinae are arranged in a horseshoe shape in *A. serratifrons,* whereas they are straight in *A. baronai.* The outer surface of the palm of the first pair of chelipeds (pereopods 1) bear scattered tufts of

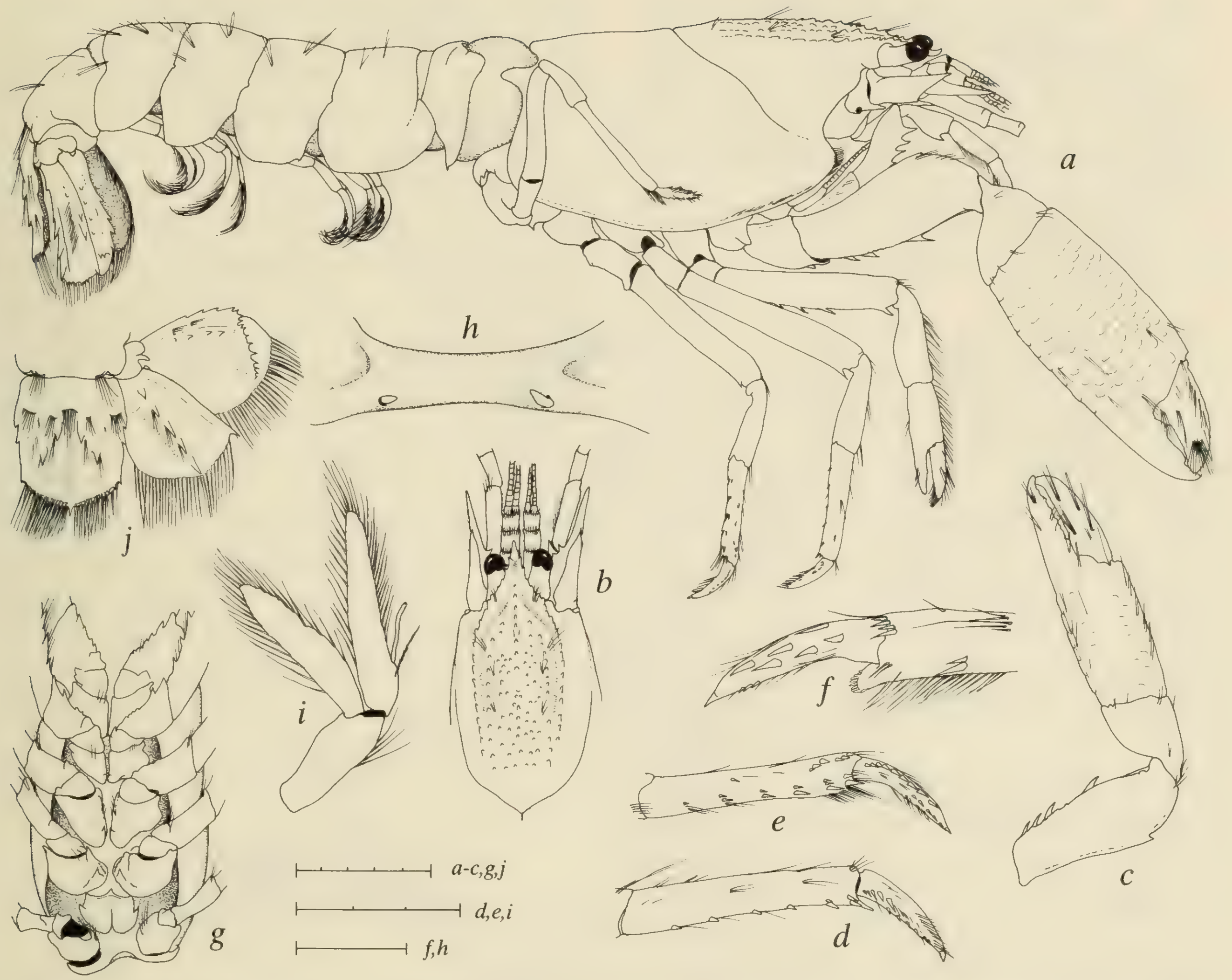

Fig. 2. *Axiopsis serratifrons* (A. Milne Edwards, 1873), ♀ (juvenile) CL 13.9 mm, Gorgona Island, USNM 251732. a, body, lateral view; b, anterior portion of carapace and cephalic appendages, dorsal view; c, left, minor cheliped (pereopod 1); d, propodus and dactyl of pereopod 3, lateral view; e, propodus and dactyl of pereopod 4, lateral view; f, distal portion of propodus and dactyl of pereopod 5, mesial view; g, sternum; h, abdominal somite 1, ventral view, showing rudimentary pleopods; i, right pleopod 2, anterior view; j, telson and right uropod, dorsal view. Scales equal 5 mm (a–c, g, j), 3 mm (d, e, i), and 1 mm (f, h).

setae in *A. serratifrons,* whereas in *A. baronai* the outer surface is densely covered with tufts of setae. The third maxilliped of *A. serratifrons* has two to three strong spines on the ventral margin that are lacking in *A. baronai.* The telson of *A. serratifrons* has three submarginal spines laterally on the distal margin, whereas these spines are absent in *A. baronai.*

Axiopsis serratifrons has long been recognized to be widely distributed in the Indo-Pacific, and more recently has also been recorded in the western Atlantic (Kensley 1981) and Ascension Island, in the central Atlantic (Manning & Chace 1990). The species, however, had not been previously recorded in the eastern Pacific, and its presence here provides further evidence of its broad, pantropical distribution.

Family Callianassidae Dana, 1852
Corallianassa xutha Manning, 1988

Corallianassa xutha Manning, 1988:885, fig. 3a–l.—Manning & Felder, 1991:777, figs. 1, 2, 5.

Material examined.—Gorgona Island: 1 ♀, CL 6.2 mm, El Tractor, 18 Mar 1987,

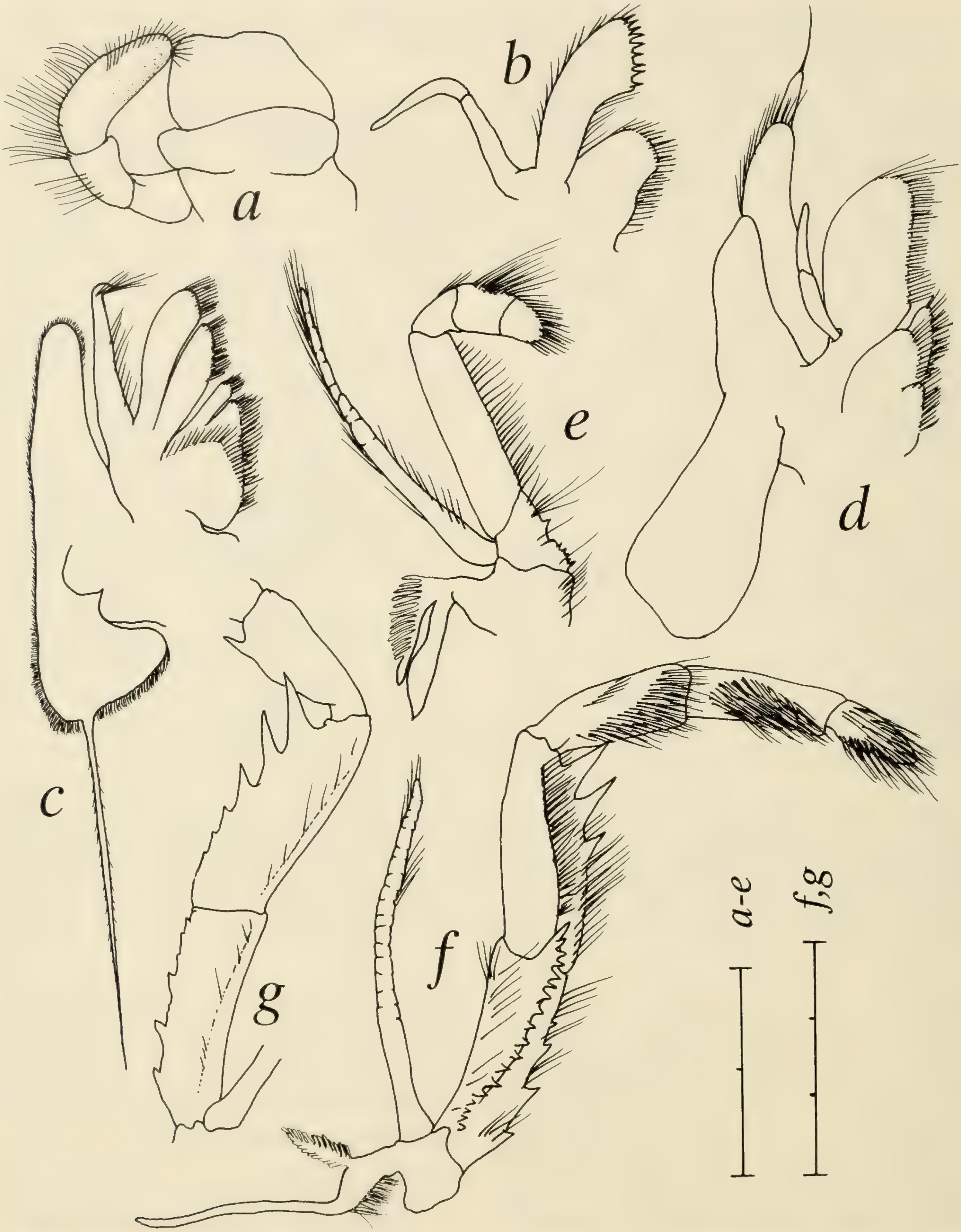

Fig. 3. *Axiopsis serratifrons* (A. Milne Edwards, 1873), ♀ (juvenile) CL 13.9 mm, Gorgona Island, USNM 251732. Mouthparts (left, all internal view except g): a, mandible; b, maxilla 1; c, maxilla 2; d, maxilliped 1; e, maxilliped 2; f, maxilliped 3; g, ischium, merus and carpus of maxilliped 3, external view (most setae omitted). Scales equal 2 mm (a–e), and 3 mm (f, g).

coll.: R. Franke, USNM 251733; 1 ♀, CL 7.4 mm, La Marranera, 1 Jul 1987, coll.: R. Franke, USNM 251734.

Color in life.—Carapace yellow, transparent, internal organs light brown. Antennules, antennae, chelipeds, and walking legs, cream white. Chelae with dark yellow chromatophores dorsally, and white ventral margin. Abdominal somites 1–5 dark yellow; abdominal somite 6 and telson transparent. Intestinal tract pink. Uropods light yellow. Pleopods dark yellow.

Habitat.—Subtidal, in burrows on rubble and broken stones.

Distribution.—Eastern Pacific: Mexico to Colombia, including Clipperton and Galápagos Islands; shore to 18 m.

Remarks.—In the description of this species Manning (1988) listed material from Colombia only from the continental coast (Ensenada de Utría). The species is now reported from Gorgona Island.

Lepidophthalmus bocourti
(A. Milne Edwards, 1870)
Fig. 4

Callianassa bocourti A. Milne Edwards, 1870:95.
Lepidophthalmus Eiseni Holmes, 1904:311, pl. 35, figs. 6–13.
Lepidophthalmus bocourti.—Manning & Felder, 1991:778.

Material examined.—Curichiche Island, Málaga Bay: 1 ♀, CL 7.0 mm, 24 Nov 1985, coll.: G. E. Ramos, USNM 251735. Gorgona Island, La Marranera: 1 ♂, CL 5.8 mm, 1 Jul 1987, coll.: R. Franke, USNM 251736.

Recognition characters.—Carapace with rostrum extending to about mid-length of eyestalks; anterolateral margins rounded. Antennular peduncle stouter than antennal peduncle, exceeding it by at least ½ length of 3rd antennular segment. Maxilliped 3 with propodus about as long as broad; dactyl slender, curved. Merus of major cheliped with spine on proximoventral margin. Pereopod 3 with dactyl subtriangular; propodus with sinuous ventral margin forming 3 lobes, outer face covered with numerous tufts of short setae. Uropod with ovate endopod distinctly longer than broad; anterior exopodal plate with row of long corneous spines on posterolateral margin (Fig. 4h). Telson broader than long, posterior margin divided into 3 lobes.

Color in life.—Carapace white, transparent; internal organs light brown with light yellow margins. Chela of pereopod 1 with red spots on dorsal surface of palm, carpus, merus and ischium; tip of fingers reddish-yellow. Antennules, antennae, and pereopods 2–5 white. Abdominal somites 1 and 2 dark yellow; abdominal somites 3–6 light yellow, with reddish band on each somite posteriorly, and numerous red chromatophores on somites and telson. Uropods lime green. Pleopods yellow.

Habitat.—Intertidal, near freshwater streams in burrows on mud or fine sediment of basaltic origin.

Distribution.—Eastern Pacific: Mexico to Colombia. Intertidal.

Remarks.—*Lepidophthalmus bocourti* is the only eastern Pacific species of *Lepidophthalmus* Holmes, 1904, a genus recently resurrected by Manning & Felder (1991). Previous to this report, *L. bocourti* was not known south of Panamá.

Neocallichirus grandimana
(Gibbes, 1850)
Fig. 5

Callianassa grandimana Gibbes, 1850: 194.—Manning, 1987:388, fig. 2.
Callianassa branneri.—Manning, 1987:388.
Neocallichirus grandimana.—Sakai, 1988: 61.—Manning & Felder, 1991:779, figs. 3, 4.

Material examined.—Gorgona Island: 1 ♂, CL 6.9 mm, 5 May 1987, coll.: R. Franke, USNM 251737.

Recognition characters.—Carapace with

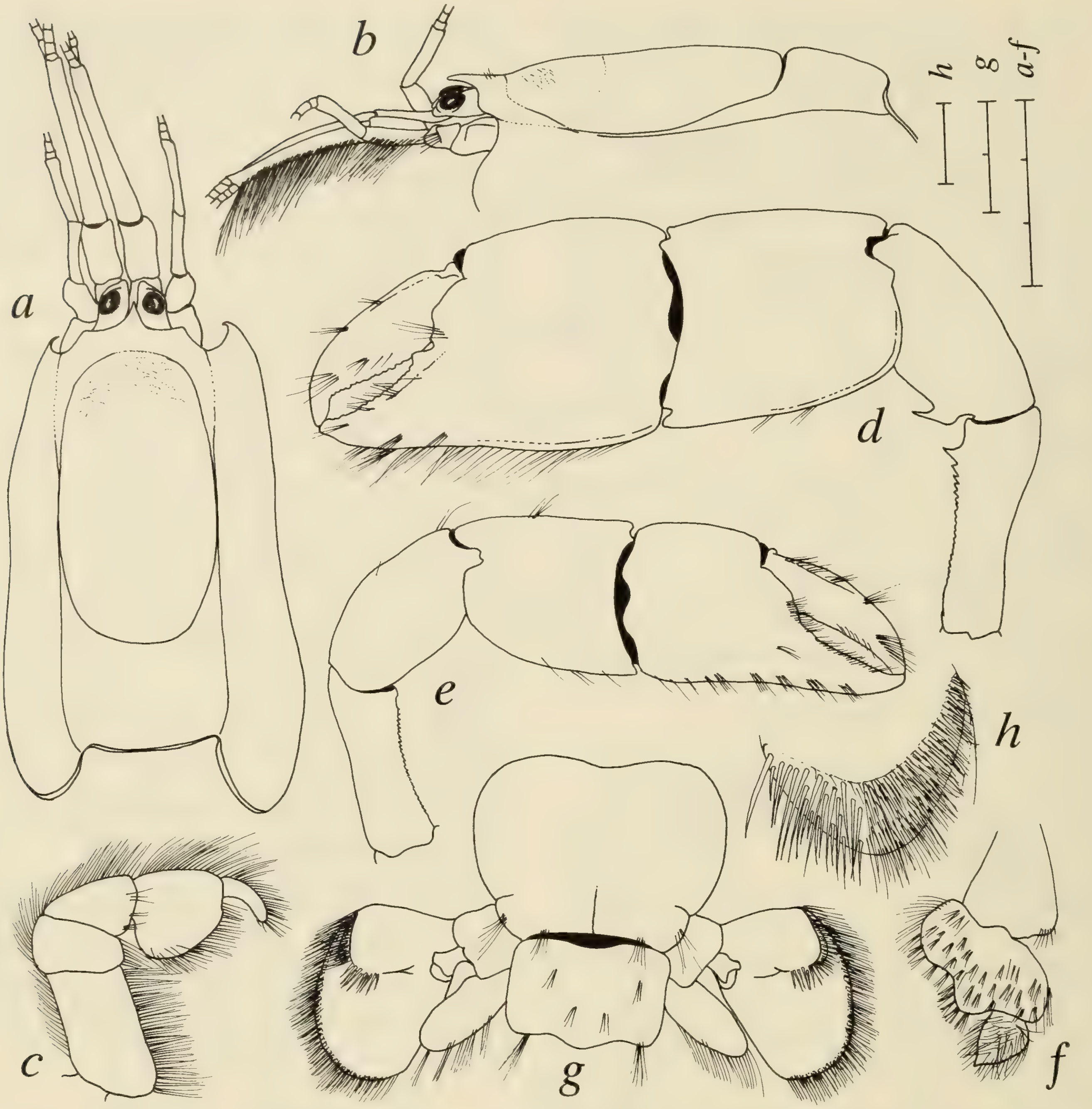

Fig. 4. *Lepidophthalmus bocourti* (A. Milne Edwards, 1870), ♀ CL 7.0 mm, Málaga Bay, USNM 251735. a, carapace and cephalic appendages, dorsal view; b, same, lateral view; c, maxilliped 3, external view; d, major cheliped (pereopod 1), lateral view; e, minor cheliped (pereopod 1), lateral view; f, propodus and dactyl of right pereopod 3, lateral view; g, abdominal somite 6, telson and uropods, dorsal view; h, posterolateral margin of right anterior exopodal plate. Scales equal 3 mm (a–f), 2 mm (g), and 0.5 mm (h).

sharp subtriangular rostrum extending to about mid-length of eyestalks; anterolateral margins broadly rounded; with dorsal oval. Antennal peduncle exceeding antennular peduncle by about ¼ length of 4th antennal segment. Third maxilliped with slender dactyl; propodus oval, as broad as long, more than twice width of dactyl. Chelipeds (pereopods 1) unequal; merus of large cheliped with ventral margin keel-like, serrate. Pereopod 3 with dactyl subtriangular, elongate; propodus with ventral margin nearly straight, outer face covered with numerous tufts of short setae. Uropod with subquadrate endopod. Telson widest on anterior margin, posterior margin weakly concave medially. Pleopods 3–5 each with appendix interna embedded in margin of endopod.

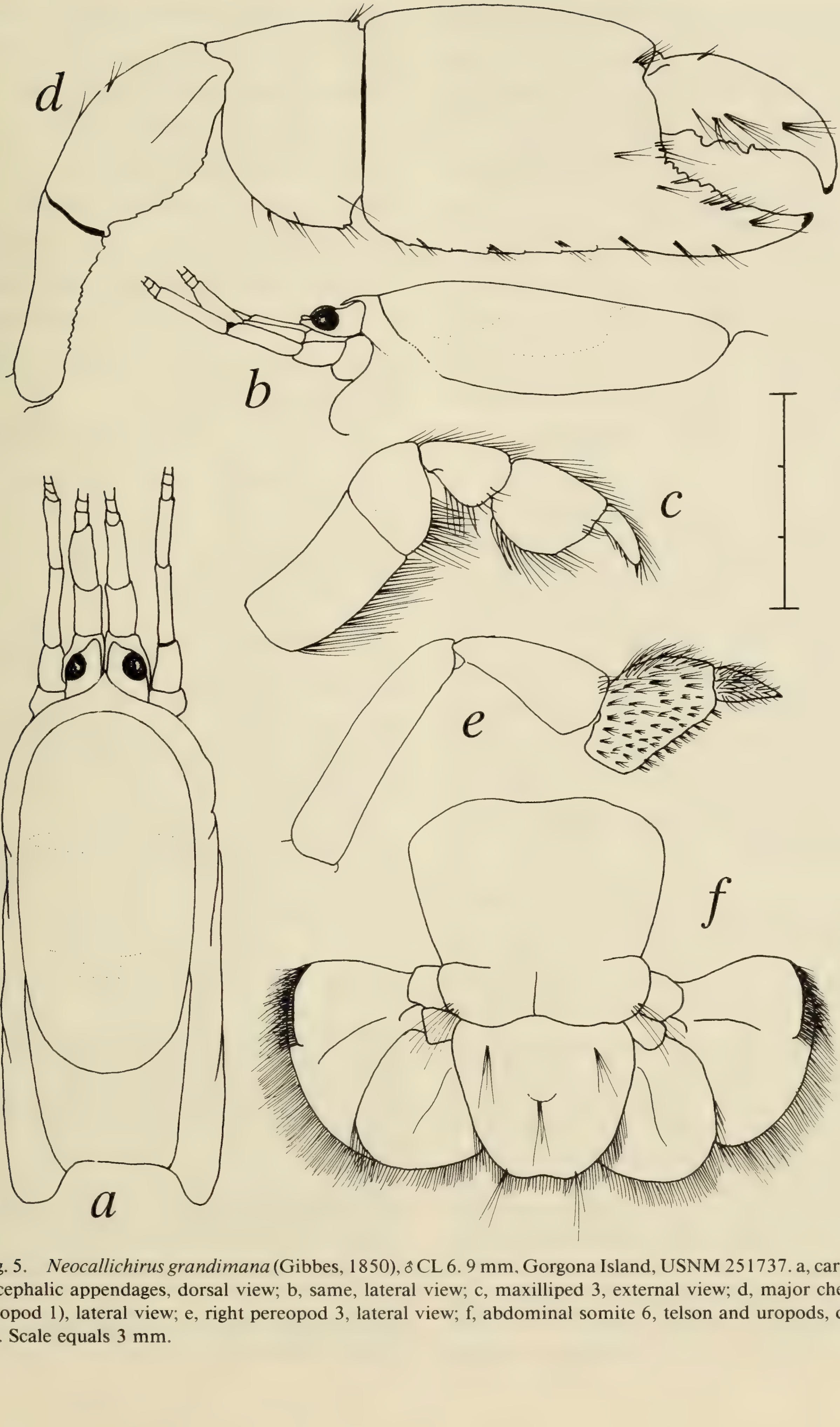

Fig. 5. *Neocallichirus grandimana* (Gibbes, 1850), ♂ CL 6. 9 mm, Gorgona Island, USNM 251737. a, carapace and cephalic appendages, dorsal view; b, same, lateral view; c, maxilliped 3, external view; d, major cheliped (pereopod 1), lateral view; e, right pereopod 3, lateral view; f, abdominal somite 6, telson and uropods, dorsal view. Scale equals 3 mm.

Habitat.—Subtidal under stones at about 1–2 m in depth.

Distribution.—Eastern Pacific: Colombia and Ecuador. Western Atlantic: southeastern Florida to Brazil, including Bermuda Islands. Intertidal to shallow subtidal.

Remarks.—*Callianassa branneri* (Rathbun, 1900), a taxon previously reported from the Pacific coast of Colombia (Prahl et al. 1979, 1990; Prahl 1986) and the western Atlantic (e.g., Rathbun 1900, Biffar 1971), was shown by Manning (1987) to be a junior synonym of *C. grandimana* Gibbes, 1850. Subsequently, Sakai (1988) transferred *C. grandimana* to the genus *Neocallichirus* Sakai, 1988. In their discussion of *C. grandimana,* Manning (1987) and Manning & Felder (1991) included only Atlantic material, leaving in question the identity of the material reported previously as *C. branneri* from the Pacific coast of Colombia. We have compared our Colombian specimen as well as additional eastern Pacific material (USNM 142536: 1 ♀, CL 12.2 mm, Salinas, Ecuador, 13 Sep 1926, coll.: W. L. Schmitt), with the neotype of *C. grandimana* from the western Atlantic (see Manning 1987:389, fig. 2), and find that the Pacific material is in agreement with it. Thus, we conclude that *N. grandimana* is indeed amphi-American in distribution.

Family Callianideidae Kossmann, 1880
Callianidea laevicauda Gill, 1859

Callianidea laevicauda.—Kensley & Heard, 1991:499, figs. 3, 4, Table 1A.

Material examined.—Gorgona Island: 1 ♂, CL 6.1 mm, La Marranera, 1 Jul 1987, coll.: R. Franke, USNM 251738; 1 ♀, CL 11.2 mm, La Ventana, 9 Sep 1987, coll.: R. Franke, USNM 251739; 1 ♀, CL 4.5 mm, El Muelle, 6 Mar 1987, coll.: R. Franke, USNM 251740; 1 ♂, CL 7.2 mm, 8 Jan 1987, coll.: C. Murillo, USNM 251741. Ensenada de Utría: 1 ♂, CL 7.1 mm, 1 juv., CL 3.4 mm, Playa Blanca Island, 14 Jul 1984, coll.: G. E. Ramos, USNM 251742.

Color in life.—Cephalothorax white, transparent, with red spots dorsally and blue chromatophores near cervical groove. Pereopods 1 and 2 red, with white stripes. Tip of fingers of chelae (pereopods 1) dark yellow. Pereopods 3–5 white, transparent. Antennular and antennal flagella with white and red bands. Abdomen white, transparent, or often abdomen and telson pink. Intestinal tract green or dark brown with black margins. Tail fan and pleopods transparent.

Habitat.—Intertidal, in burrows under stones or coralline sand. Very abundant in sandy bottoms where individuals are often seen at entrance of burrow moving their chelipeds and antennae.

Distribution.—Eastern Pacific: Socorro Island, Mexico, and Colombia. Western Atlantic: Caribbean. Intertidal to shallow subtidal.

Family Laomediidae Borradaile, 1903
Axianassa sp.

Material examined.—Ensenada de Utría: 1 ♂, CL 3.4 mm, Playa Blanca Island, 14 Jul 1984, coll.: G. E. Ramos, USNM 251743. (Specimen missing abdomen, antennules, most of antennae, and 5th pereopods.)

Habitat.—Intertidal, under stones and coralline sand.

Remarks.—Our specimen of *Axianassa* sp. could possibly represent *A. mineri* Boone, 1931, the only eastern Pacific species of the genus. According to Kensley & Heard (1990), *A. mineri* is known only from the holotype collected in the Bay of Panamá (Pacheca Island, Pearl Islands). However, because our specimen is missing structures considered of diagnostic importance (i.e., antennal acicle, abdomen), it has not been possible to identify it with certainty to the species level.

Family Upogebiidae Borradaile, 1903
Pomatogebia rugosa (Lockington, 1878)

Upogebia rugosa.—Williams, 1986:58, fig. 21.

Pomatogebia rugosa.—Williams & Ngoc-Ho, 1990:616.

Material examined.—Playa Pizarro, Gorgona Island: 1 ♀ ovig., CL 5.1 mm, 12 Jan 1987, coll.: R. Franke, USNM 251744; 1 ♂, CL 3.6 mm, 12 Apr 1987, coll.: R. Franke, USNM 251745.

Habitat.—Subtidal, between branches or heads of *Pocillopora* corals.

Distribution.—Previously known only from Baja California. The discovery of *Pomatogebia rugosa* in Colombia represents a considerable southward range extension for this species. Subtidal to about 18 m.

Upogebia maccraryae Williams, 1986

Upogebia maccraryae Williams, 1986:27, fig. 10.

Material examined.—Tumaco, Department of Nariño: 9 ♀ (4 ovigs.), CL 7.8–8.6 mm, 28 Nov 1981, coll.: H. von Prahl, USNM 251746. Playa Basura, Buenaventura Bay: 1 ♂ CL 5.7 mm, 1 ♀ ovig. CL 7.0 mm, 8 Jun 1989, coll.: J. R. Cantera, CRBMUV 89019.

Habitat.—Intertidal, in burrows on mud near mangroves.

Distribution.—Eastern Pacific: El Salvador to Ecuador; 3–5.4 m.

Remarks.—Although the Colombian coast is within the range of this species, it had not been previously reported from this coast.

Upogebia spinigera (Smith, 1871)

Upogebia spinigera.—Williams, 1986:41, fig. 15.

Material examined.—Aguacate Bay, Department of Chocó: 1 ♀ ovig., CL 7.6 mm, 2 juvs., CL 3.8, 4.6 mm, 15 Jul 1986, USNM 251747. Rampa de Los Suecos, Málaga Bay: 2 ♂ CL 6.0–8.9 mm, 1 ♀ CL 5.3 mm, 27 Dec 1985, coll.: G. E. Ramos, CRBMUV 85069. Cangrejo Island, Buenaventura Bay: 2 ♂ CL 7.2–8.9 mm, 1 ♀ CL 7.5 mm, 1 ♀ ovig. CL 8.8 mm, 11 Dec 1986, coll.: R. Neira, CRBMUV 86032.

Color in life.—Carapace, abdomen, pereopods 2–5, and tail fan transparent. Pereopods 1 white, transparent, tips of fingers dark brown. Setae on body, antennules and antennae very light brown.

Habitat.—Intertidal, in holes on wood stranded on beach, or in burrows on rocky shores. Often captured along with the shrimp *Alpheus bouvieri* A. Milne Edwards.

Distribution.—Eastern Pacific: Golfo de Fonseca to Ecuador; intertidal to shallow subtidal.

Remarks.—The only previous report of this species from Colombia is from Buenaventura (Holthuis 1952).

Upogebia tenuipollex Williams, 1986

Upogebia tenuipollex Williams, 1986:45, fig. 16.

Material examined.—Málaga Bay: 5 ♀ (1 ovig.), CL 4.8–8.1 mm, 4 ♂, CL 5.5–6.6 mm, Curichiche Island, 26 Feb 1986, coll.: G. E. Ramos, USNM 251748; 4 ♂ CL 4.5–6.3 mm, 1 ♀ CL 7.1 mm, 1 ♀ ovig. CL 6.7 mm, 12 Nov 1981, coll.: H. von Prahl, CRBMUV 81086; 1 ♂ CL 8.0 mm, La Sierpe, 25 Dec 1985, coll.: G. E. Ramos, CRBMUV 85032; 1 ♀ CL 9.8 mm, Cangrejo Island, 11 Dec 1986, coll.: R. Neira, CRBMUV 86006. Gorgona Island: 1 ♂ CL 7.0 mm, 1 ♀ CL 8.1 mm, Gorgonilla, 8 Jan 1987, coll.: C. Murillo, CRBMUV 87007; 1 ♀ ovig. CL 8.5 mm, Gorgonilla, 29 Jan 1987, coll.: R. Franke, CRBMUV 87008; 1 ♂ CL 8.7 mm, El Tractor, 18 Mar 1987, coll.: R. Franke, CRBMUV 87009; 2 ♀ CL 8.6–9.2 mm, El Tractor, 25 Jun 1987, coll.: R. Franke, CRBMUV 87011; 2 ♂ CL 5.4–6.6 mm, 1 ♀ CL 10.1 mm, Playa Pizarro, 16 May 1988, coll.: H. von Prahl, CRBMUV 88010.

Color in life.—Carapace and abdomen white, transparent, or often light yellow with a blue chromatophore spot on cervical groove. Carapace sometimes light brown on dorsal surface. Setae on chelipeds, pereopods, and tail fan lemon yellow. Eggs of ovigerous females orange.

Habitat.—Intertidal, in burrows and crevices on broken stones, rubble, or on roots of mangroves.

Distribution.—Eastern Pacific: Colombia to Ecuador; intertidal to 3.6 m.

Remarks.—The species was previously known only from Ecuador.

Upogebia thistlei Williams, 1986

Upogebia thistlei Williams, 1986:47, fig. 17.

Material examined.—El Tractor, Gorgona Island: 1 ♀ CL 7.3 mm, 18 Mar 1987, coll.: R. Franke, CRBMUV 87010.

Habitat.—Intertidal, in rubble.

Distribution.—Eastern Pacific: Gulf of California to northern Ecuador; intertidal to shallow subtidal.

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Appendix

Checklist of species of Thalassinidea from the eastern Pacific, with their known geographic and bathymetric distribution, past generic placement, and common synonyms. (Based primarily on: Williams 1986; Hendrickx 1987; Kensley 1989; Sakai & De Saint Laurent 1989; Kensley & Heard 1990, 1991; Manning & Felder 1991.)* = species known to occur on the Pacific coast of Colombia.

Family Axiidae Huxley, 1878

Genus *Acanthaxius* Sakai & De Saint Laurent, 1989

*1. *A. caespitosa* (Squires, 1979): Gulf of California, and Colombia; 72–200 m. (Previously in the genus *Axiopsis* Borradaile, 1903).

2. *A. spinulicauda* (Rathbun, 1902): British Columbia, Puget Sound, and California; 70–255 m. (Previously in the genus *Axiopsis* Borradaile, 1903.)

Genus *Axiopsis* Borradaile, 1903

*3. *A. baronai* Squires, 1977: Gulf of California, Colombia, and Perú; 5–9 m.

*4. *A. serratifrons* (A. Milne Edwards, 1873): in the eastern Pacific from Colombia; Indo-Pacific; Red Sea; western and South Atlantic; shallow subtidal to about 17 m.

Genus *Calocarides* Wollebaek, 1908

5. *C. quinqueseriatus* (Rathbun, 1902): British Columbia, Oregon, and California; 228–2200 m. (Previously in the genus *Calastacus* Faxon, 1893.)

Genus *Eiconaxius* Bate, 1888

6. *E. acutifrons* Bate, 1888: in the eastern Pacific from the Bay of Panamá; Indo-Pacific; 595–1015 m. (Previously in the genus *Axius* Leach, 1815.)

7. *E. cristagalli* (Faxon, 1893): south of Panamá; 850 m. (Previously in the genus *Axius* Leach, 1815.)

Genus *Neaxius* Borradaile, 1903

*8. *N. frankeae*, new species: Gorgona Island (Colombia); shallow subtidal.

9. *N. vivesi* (Bouvier, 1895): Baja California, Gulf of

California, and Panamá; 5–7 m (Previously in the genus *Axius* Leach, 1815.)

Family Calocarididae Ortmann, 1891
Genus *Calocaris* Bell, 1853

10. *C. granulosa* Grebenyuk, 1975: Bay of Alaska; 756–1000 m.

Genus *Calastacus* Faxon, 1893

11. *C. rostriserratus* Andrade & Baez, 1977: off Valparaiso (Chile); 320–400 m.

12. *C. stylirostris* Faxon, 1893: off Acapulco (Mexico), and Bay of Panamá; 1098–1220 m.

Genus *Lophaxius* Kensley, 1989

13. *L. rathbunae* Kensley 1989: northeastern Pacific from Alaska to California; 549–1190 m. [Kensley (1989: 963) determined that eastern Pacific records of *Calastacus investigatoris* Anderson, 1896, are actually *L. rathbunae*.]

Family Callianassidae Dana, 1852

Genus *Callichirus* Stimpson, 1866

14. *C. seilacheri* (Bott, 1955): El Salvador to Chile; intertidal. (Previously in the genus *Callianassa* Leach, 1814.)

Genus *Corallianassa* Manning, 1987

*15. *C. xutha* Manning, 1988: Mexico to Colombia, including Clipperton and Galápagos Islands; shore to 18 m.

Genus *Lepidophthalmus* Holmes, 1904

*16. *L. bocourti* (A. Milne Edwards, 1870): Mexico to Colombia; intertidal. (Previously in the genus *Callianassa* Leach, 1814; =*Lepidophthalmus eiseni* Holmes, 1904).

Genus *Neocallichirus* Sakai, 1988

*17. *N. grandimana* (Gibbes, 1850): Panamá to Ecuador; intertidal to shallow subtidal. [Previously in the genus *Callianassa*; =*Callianassa branneri* (Rathbun, 1900).]

Genus *Neotrypaea* Manning & Felder, 1991

18. *N. californiensis* (Dana, 1854): Alaska to Baja California; intertidal. (Previously in the genus *Callianassa* Leach, 1814.)

19. *N. gigas* (Dana, 1852): British Columbia to Baja California; intertidal to shallow subtidal. (Previously in the genus *Callianassa*; =*Callianassa longimana* Stimpson, 1857.)

20. ?*N. rochei* (Bouvier, 1895): Baja California; probably intertidal. (Generic placement uncertain, see Manning & Felder 1991:792.)

21. *N. uncinata* (H. Milne Edwards, 1837): Chile; intertidal to shallow subtidal. (Previously in the genus *Callianassa* Leach, 1814.)

Genus *Notiax* Manning & Felder, 1991

22. *N. brachyophthalma* (A. Milne Edwards, 1870): Chile, Argentina; subtidal. (Previously in the genus *Callianassa* Leach, 1814.)

Family Ctenochelidae
Manning & Felder, 1991
Genus *Callianopsis* De Saint Laurent, 1973

23. *C. goniophthalma* (Rathbun, 1902): Alaska to California; 480–650 m. (Previously in the genus *Callianassa* Leach, 1814.)

Family Callianideidae Kossmann, 1880
Genus *Callianidea* H. Milne Edwards, 1837

*24. *C. laevicauda* Gill, 1859: in the eastern Pacific from Baja California, and Socorro Island (Mexico), to Colombia, and the Galápagos Islands; in the western Atlantic from the Caribbean; intertidal to shallow subtidal.

Family Laomediidae Borradaile, 1903
Genus *Axianassa* Schmitt, 1924

25. *A. mineri* Boone, 1931: Bay of Panamá; intertidal.

26. *A. canalis* Kensley & Heard, 1990: Panamá Canal; subtidal.

*27. *A.* sp. (reported herein).

Family Upogebiidae Borradaile, 1903
Genus *Pomatogebia*
Williams & Ngoc-Ho, 1990

28. *P. cocosia* (Williams, 1986): Cocos Islands (Costa Rica); subtidal. (Previously in the genus *Upogebia* Leach, 1814.)

*29. *P. rugosa* (Lockington, 1878): Baja California, and Colombia; subtidal to about 18 m. (Previously in the genus *Upogebia* Leach, 1814.)

Genus *Upogebia* Leach, 1814

30. *U. acanthops* Williams, 1986: Panamá; 1 m.

31. *U. affinis* (Say, 1818): in the eastern Pacific from California (introduced); in the western Atlantic from Massachusetts to Brazil; intertidal to 29 m.

32. *U. burkenroadi* Williams, 1986: Sonora (Mexico); shallow subtidal.

33. *U. dawsoni* Williams, 1986: Baja California to Panamá; intertidal.

34. *U. galapagensis* Williams, 1986: Galápagos Islands; intertidal.

35. *U. jonesi* Williams, 1986: Baja California to Panamá; intertidal to 72 m.

36. *U. lepta* Williams, 1986: Santa Catalina Islands (California) and Los Coronados Islands (Baja California); 72–101 m.

37. *U. longipollex* (Streets, 1871): El Salvador to Ecuador; intertidal.

*38. *U. maccraryae* Williams, 1986: El Salvador to Ecuador; 3–5.4 m.

39. *U. macginitieorum* Williams, 1986: California; intertidal.

40. *U. onychion* Williams, 1986: California; 37.8 m.

41. *U. pugettensis* (Dana, 1852): Alaska to California; intertidal to several fathoms.

42. *U. ramphula* Williams, 1986: Nayarit (Mexico); 7.2–18 m.

43. *U. schmitti* Williams, 1986: Panamá; subtidal.

*44. *U. spinigera* (Smith, 1871): Golfo de Fonseca to Ecuador; intertidal to shallow subtidal.

*45. *U. tenuipollex* Williams, 1986: Colombia, and Ecuador; intertidal to 3.6 m.

*46. *U. thistlei* Williams, 1986: Gulf of California to Ecuador; intertidal to shallow subtidal.

47. *U. veleronis* Williams, 1986: Islas Tres Marias (Mexico), and Ecuador; 3.6–23.4 m.

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PROCAMBARUS (*ORTMANNICUS*) *ATTIGUUS*, A NEW TROGLOBITIC CRAYFISH (DECAPODA: CAMBARIDAE) FROM THE SAINT JOHNS RIVER BASIN, FLORIDA

Horton H. Hobbs, Jr. and Richard Franz

Abstract.—*Procambarus* (*Ortmannicus*) *attiguus*, an albinistic troglobite, is described from Silver Glen Springs, 14.4 km northwest of Astor Park, Marion County, Florida. Its closest affinities are with *P.* (*O.*) *delicatus* Hobbs & Franz, the two sharing several unusual characteristics, including enlarged third maxillipeds, with the monotypic Floridian troglobite *Troglocambarus maclanei* Hobbs. The combination of denticles on the opposable margin of the ischium of the enlarged third maxilliped and the areola less than 20 times as long as broad distinguishes the new species from other members of the Cambaridae.

Procambarus (*Ortmannicus*) *attiguus*, described herein from Silver Glen Springs, Marion County, Florida, is another crayfish sharing a character (enlarged third maxillipeds) that prior to the discovery of *Procambarus* (*Ortmannicus*) *delicatus* Hobbs & Franz (1986) was believed to be unique to the monotypic *Troglocambarus maclanei* Hobbs, 1942. As in *P.* (*O.*) *delicatus*, however, there are denticles (lacking in *T. maclanei*) on the opposable margin of the ischium of this appendage that are fewer in number, more delicate, and more acute than in other troglobitic or epigean cambarids. The new species is the only member of the subfamily Cambarinae, except for *T. maclanei*, that at least sometimes lacks a posterior arthrobranch on segment XIII, that bearing the fourth pereiopod. The sometimes absence of this gill, the broader areola, and the reduced (not visible in dorsal aspect) pouch-like protrusion on the anteroventral surface of the branchiostegites distinguish this crayfish from its closest relative, *P.* (*O.*) *delicatus*.

Procambarus (*Ortmannicus*) *attiguus*, new species

Diagnosis.—Albinistic; eyes reduced and without facets or pigment. Rostrum lacking marginal spines and median carina. Carapace with reduced pouch-like protrusions in anteroventral branchiostegal regions but lacking cervical spines. Areola 13.6 to 15.9 times as long as broad and constituting 40.0 to 41.7% of total length of carapace (49.7–51.9% of postorbital carapace length). Suborbital angle absent. Postorbital ridge without spines or tubercles. Antennal scale about 1.7 times as long as broad, broadest distal to midlength. Third maxillipeds enlarged, opposable margin of ischium with 7 to 9 denticles and as many as 8 small tubercles or spines laterally, distolateral extremity with spine. Ischia of third and fourth pereiopods with digitiform hooks, that of third overreaching basioischial articulation, neither opposed by tubercle on corresponding basis; coxa of fourth pereiopod with prominent boss, that of fifth lacking boss. First pleopods of first form male asymmetrical, reaching coxae of third pereiopods; distal extremity lacking subapical setae but bearing: spiculiform mesial process, which directed distolaterally and slightly inclined caudally, reaching about same distance distally as central projection; cephalic process tapering, acute, directed distally but weakly bowed cephalically, its apex falling short of apex of central projection; caudal process, smallest of terminal elements, slender, acute, directed distally, and reaching slightly beyond midlength of central projection; and latter, largest of terminal elements, bladelike, acute, and disposed distally but inclined slightly caudally. Annulus ventralis freely movable, subovate, about 1.7 times as broad as long, completely exposed even though preannular sternite with 2 pairs of low elevations flanking caudal margin; convex ventral surface with prominent median longitudinal furrow much expanded, especially dextrally, posterior to midlength; flanking dextral ridge with large, anteriorly situated depression, narrower sinistral one broken by oblique furrow anterior to midlength; sinus, with anterior extremity situated in cephalic part of furrow, extending caudally and slightly sinistrally across median line before gently curving caudodextrally far beyond median line where turning caudosinistrad and ending near caudal margin of annulus slightly dextral to median line; fossa scarcely evident but situated at about midlength of sinus. Postannular sclerite approximately 0.7 as broad as annulus and about 0.5 as long. First pleopod of female represented by very small tuberculiform rudiment.

Holotypic male, form I.—Cephalothorax subovate in cross section, weakly depressed (Fig. 1a, d). Abdomen slightly narrower than thorax (10.0 and 12.3 mm). Greatest width of carapace greater than height at caudodorsal margin of cervical groove. Areola 15.9 times as long as wide with room for 1 or 2 punctations in narrowest part. Cephalic section of carapace 2.4 times as long as areola, length of latter 41.7% of entire length of carapace (51.9% of postorbital carapace length). Rostrum with convergent, nonthickened margins. Acumen, not clearly delimited basally, reaching base of ultimate podomere of antennular peduncle; dorsal surface excavate and sparsely punctate. Subrostral ridge weak and evident in dorsal aspect only at base, joining lateral rostral carina at about midlength of penultimate podomere of antennular peduncle (Fig. 1a, d). Postorbital ridges lacking spines and tubercles. Cervical spines lacking, tubercles in area no larger than others on branchiostegites. Branchiostegal spines absent. Almost entire surface of carapace except for dorsomedian and extreme anterolateral areas granulate. Paired pouchlike protrusions on anteroventral branchiostegal region present but much less conspicuous than in *Procambarus* (*O.*) *delicatus* and not visible in dorsal aspect of carapace.

Abdomen only slightly shorter than carapace. Pleura of third through fifth abdominal segments rounded anteroventrally, subangular posteroventrally. Cephalic section of telson with single fixed spine in each caudolateral corner. Cephalic lobe of epistome (Fig. 1e) subtriangular, with cephalolateral margins weakly elevated (ventrally); main body with depressed anteromedian area bearing distinct fovea; epistomal zygoma broadly arched.

Ventral surface of proximal podomere of antennular peduncle with submedian spine distal to midlength. Antennal peduncle lacking spines and tubercles but acute angle present on distolateral margin of basis; flagellum extending beyond caudal margin of telson by more than length of latter. Antennal scale (Fig. 1o) 1.7 times as long as broad, widest distinctly distal to midlength, and lamellar area about 3 times as wide as thickened lateral part. Right mandible (Fig. 1h) with incisor ridge bearing 10 denticles, cephalic molar process very weakly corneous, shallowly concave; caudal molar process with 3 cusps, 2 of which corneous-tipped, at angles of triangle. Third maxillipeds (Fig. 1a, k) enlarged, overreaching rostrum by combined length of dactyl, propodus, and little more than half that of carpus; ischium with lateral margin bearing 6 (sinistral) or 9 (dextral) spiniform tubercles; opposable margin with 7 (dextral) or 9 (sinistral) spiniform denticles; lateral half of ventral surface with clusters of minute setae; exopod reaching base of distal fourth of merus.

Left chela (Fig. 1j. Note: many tubercles

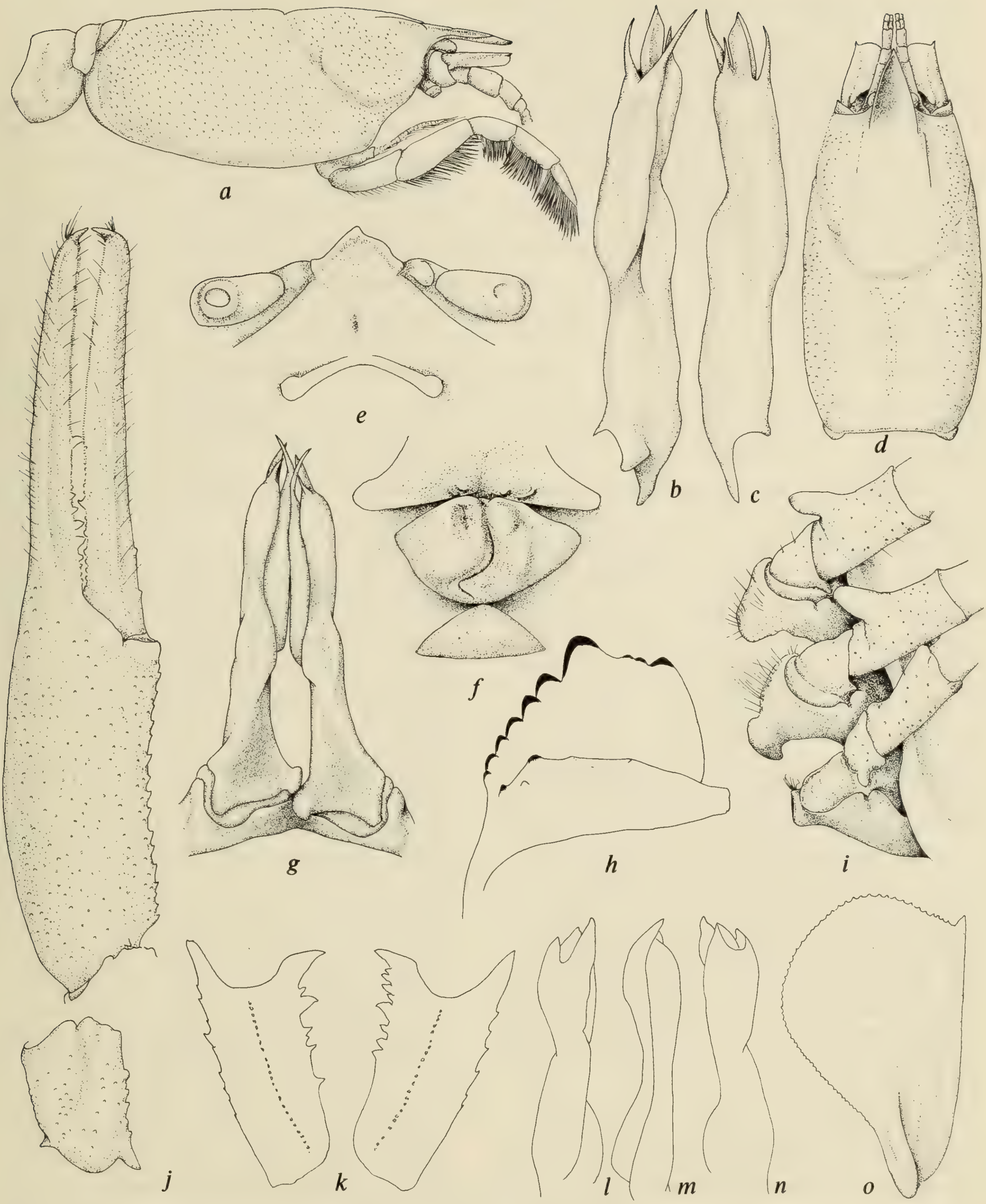

Fig. 1. *Procambarus* (*O.*) *attiguus,* new species (all from holotype except f from allotype and l–n from form II exuvia of holotype). a, Lateral view of carapace, basal podomeres of antenna, third maxilliped, and first two abdominal segments; b, Mesial view of left first pleopod; c, Lateral view of same; d, Dorsal view of carapace; e, Epistome and part of basal antennal podomere; f, Annulus ventralis and adjacent sternal elements; g, Caudal view of first pleopods; h, Caudal view of dextral mandible; i, Basal podomeres (coxa-ischium) of third, fourth, and fifth pereiopods; j, Dorsal view of distal podomeres (carpus-dactyl) of left cheliped; k, Ventral (postaxial) view of ischia of third maxillipeds; l, Mesial view of first pleopod; m, Caudal view of same; n, Lateral view of same; o, Antennal scale.

enumerated in the description are too small to be included in the illustration) subovate in cross section, not strongly depressed. Mesial surface of palm with at least 3 irregular rows of 12–15 tubercles, some of which acute; other surfaces also studded with tubercles. Fingers provided with well-defined ridges dorsally and ventrally; dorsal ridges flanked by few small tubercles proximally and by setiferous punctations along remainder of fingers. Opposable margin of fixed finger with 2 rows of tubercles: upper consisting of 10 tubercles (fifth and sixth from base subequal in size and larger than others) extending from base of finger almost to base of middle third of length; lower row of 4 tubercles (third from base decidedly largest) in middle third of finger (corresponding numbers on right chela 15 and 5); longitudinal band of minute denticles extending between more distal tubercles and continuing uninterrupted to base of corneous tip of finger; lateral margin of finger with row of 3 small tubercles along proximal sixth followed by row of setiferous punctations. Opposable margin of dactyl with 2 rows of tubercles: upper of 20 (sixth from base largest) along proximal half of finger and lower row of 4 (proximalmost largest) in distal part of proximal half of finger (corresponding numbers on right chela 18 and 4); longitudinal band of minute denticles extending between tubercular rows and beyond, reaching base of corneous tip; mesial margin of dactyl with only 2 tubercles representing usual row, these followed distally by row of setiferous punctations.

Carpus of left cheliped (Fig. 1j) longer than broad, tuberculate; prominent subacute tubercles on median ventrodistal margin, that on ventrolateral condyle no larger than others nearby; shallow oblique sulcus on dorsal surface flanked by squamous tubercles.

Merus of left cheliped studded with tubercles except mesially and laterally where sparse except distally. Usual mesial and lateral rows on ventral surface irregular but consisting of 30 or 33 tubercles of varying, not graduated, sizes. Ischium with row of 6 tubercles along mesial margin.

Hooks on ischia of third and fourth pereiopods (Fig. 1i) digitiform, that on third overreaching basioischial. Coxa of fourth pereiopods with prominent boss; no boss present on coxa of fifth pereiopod.

Sternum between third and fourth pereiopods moderately deep; ventrolateral margins setiferous but not forming conspicuous mat; sternite between fifth (not "fourth" as erroneously noted in the description of *P.* (*O.*) *delicatus*, Hobbs & Franz, 1986:512) pereiopods not produced in conspicuous, median, tuberculiform prominence. First pleopods (Fig. 1b, c, g) as described above in "Diagnosis." First pleopod from exuviae of holotype (see Fig. 1l, m, n), although somewhat distorted, revealing features of appendage of second form male. Uropods with both lobes of basal podomere ending in spines; distomedian spine on mesial ramus situated some distance proximal to distal margin of ramus. (See Table 1 for measurements.)

Branchial count, determined from exuvia of holotype, 17 + ep.

Allotypic female.—Excluding secondary sexual features, allotypic female differing from holotype as follows: areola 13.6 times as long as wide and comprising 40.3% of postorbital length; apex of rostrum reaching midlength of ultimate podomere of antennular peduncle; pouchlike protrusions on cephaloventral region of branchiostegites reduced, even less noticeable; mandible with 11 denticles on incisor ridge; opposable margins of ischia of right and left third maxillipeds with 7 and 9 spiniform denticles, respectively; chelipeds missing. See "Diagnosis" for description of annulus ventralis and adjacent sternal area (Fig. 1f). (Also, see Table 1.)

Notes on the paratypic juvenile female.—This specimen was obviously involved in an unfortunate mishap. All of the appendages, except the mandibles through the second maxillipeds, have been subjected to some degree of mutilation and most bear at least regenerative buds. The rostrum is slightly longer than those of the primary types and, although apically abraded, almost reaches the end of the antennular peduncle. Also, the cephalic section of the telson bears a small movable spine immediately mesial to the fixed dextral one. The branchial series was examined only on the right side and, unlike the holotype, lacks a posterior arthrobranch at the base of the fourth pereiopod. As noted in Table 1, other slight differences occur in the proportions of features of the carapace.

Type locality.—Silver Glen Springs, 9 mi (14.4 km) northwest of Astor Park, Marion County, Florida (SE ¼, NE ¼, SE ¼, Sec. 25 T.14S, R. 26E). The springs at Silver Glen are located in a semicircular pool which forms a wide spring run that flows eastward into Lake George and the St. Johns River. Most of the flow discharges from two large openings, although some water emerges from numerous sand boils in the main spring run and in a small tributary that enters the pool on the southwest side. A large vertical solution tube, known as the "Natural Well," discharges water from a small cave passage into the northwest corner of the pool. The entrance to the main system lies in approximately 6.5 m of water on the northeast side of the spring pool. The initial passage is a tight maze that opens into a large room approximately 55 m from the entrance. The passage from the Natural Well entrance intercepts the main cave through a large breakdown pile of limestone rubble on the floor of this room. The main cave continues to a large room about 213 m from the main entrance. The floor of this room is at a water depth of 49 m; the ceiling is at 15 m.

The crayfish were found in the latter room where several were sequestered in small crevices in the walls. Two individuals, however, were seen floating in the water column about 30 m above the floor and were presumably displaced from the ceiling by bubbles of air escaping from the divers' regulators. One individual was observed on an extensive flocculence of reddish organic material, possibly bacterial growth, on a breakdown slope near the floor of the room. Others were seen moving on the bottom away from these clusters. Because of the strong outflow, there is no visible accumulation of organic detritus anywhere in the cave. Unidentified amphipods were seen in the cave and large numbers of redeye chubs (*Notropis harperi*) were observed in sheltered areas throughout the cave. American eels (*Anquila rostrata*), large shrimps (*Macrobrachium carcinus*), and blue crabs (*Callinectes sapidus*) occurred at both major cave vents, but were not observed in the cave. Striped bass (*Morone saxatilis*), which frequently appear in the vicinity of the main entrance, followed the divers on several occasions deep into the cave system.

Passages in this system exhibit strong outflows of water, making entry very difficult. An average discharge of 112 ft^3 (3.1 m^3)/sec

Table 1.—Measurements (mm) of *Procambarus* (*O.*) *attiquus*, new species.

	Holotype	Allotype	Paratype
Carapace			
Entire length	26.2	23.6	17.0
Postorbital length	21.4	19.1	13.6
Width	12.3	10.6	7.5
Height	11.0	9.2	6.9
Areola			
Width	0.7	0.7	0.5
Length	11.1	9.5	6.8
Rostrum			
Width	4.2	3.1	2.3
Length	5.5	5.9	3.7
Left Chela			
Length, palm mesial margin	10.0		
Palm width	5.2		
Length, lateral margin	25.5		
Dactyl length	14.4		
Abdomen			
Width	10.0	8.4	6.6
Length	25.6	22.5	18.2

and a maximum outflow of 129 ft^3 (3.7 m^3)/sec in April 1935 were reported by Rosenau et al. (1977). Like other spring discharges in the Lake George area, the chemical composition of Silver Glen Springs water includes high concentrations of calcium, magnesium, sodium, sulfates, and chlorides (see Rosenau et al. (1977).

The Silver Glen Springs cave system is believed to have developed along the contact between the (Miocene) Hawthorn Group and the older (Eocene) Ocala Limestones. Both entrances and the maze portion of the main cave are in sediments that may represent the Coosawhatchee Formation. According to Scott (1988), this is the upper formation in the Hawthorn Group and lies above the Marks Head and Penney Farms formations. He also noted that in the vicinity of Lake George, the Hawthorn Group sequence of sediments is compressed into a thin layer probably no more than 75 ft (22.9 m) thick. It rests unconformably on the Ocala Limestones, probably the Crystal River Formation, approximately 300 m below the surface.

The specimens were collected by Tom Morris on 6 February and 16 August 1990 and were maintained in aquaria until they died, the holotype (following three molts) on 13 January 1991. A more detailed account of the locality and of the maintenence of the specimens is being prepared by the second author and Tom Morris in their review of the troglobitic crayfishes of the St. Johns River Basin.

Disposition of types.—The holotypic male, form I, the allotype, and the juvenile female paratype are deposited in the National Museum of Natural History (Smithsonian Institution), numbers 220683, 220684, 220685, respectively.

Size.—The holotype is the largest of the three known specimens. Its carapace length is 26.6 mm, its postorbital carapace length 21.4 mm. Corresponding lengths of the allotypic female are 23.6 and 19.1 mm.

Range.—This crayfish is known only from the type locality.

Relationships.—There seems to be no question that this new crayfish has its closest affinities with *Procambarus* (*Ortmannicus*) *delicatus* and, more distantly, with *Troglocambarus maclanei.* It shares so many features in common with *delicatus* that we have some reluctance in choosing not to consider the specimens at hand to be conspecific with the latter, the only known representatives of which were taken from nearby Alexander Springs, Lake County—the two populations are separated by no more than 15 airmiles. But the crucial features of the first pleopod of the first form male of *delicatus* are unknown, the species having been described on the basis of two second form males and a female. Inasmuch as there are several features that make the specimens from Silver Glen Springs readily distinguishable from those of *delicatus* from Alexander Springs and the likelihood that the first pleopod of first form males of the latter (when they become available) will reveal further differences we have decided to recognize the two populations as representing distinct species. The features that set these three specimens apart from *delicatus* are as follows: thorax less inflated and not quite so strongly tuberculate; areola 13.6 to 15.9 (as opposed to 25.5 to 30.7) times as long as broad, and constituting 40.0 to 41.7% (as opposed to 43.8 to 46.6%) of total length of carapace; mandible with major denticle on incisor ridge fourth or fifth (as contrasted with third) from lateral side; opposable margin of ischium of third maxilliped with row of 7 to 9 (as opposed to 5 to 7) denticles; pouchlike protrusions on anteroventral branchiostegal region much reduced and not visible in dorsal aspect; mesial process of first pleopod of second form male more robust and cephalic process comparatively longer (viewed laterally overreaching midlength of centrocephalic process of central projection, as opposed to falling short of midlength);

annulus ventralis somewhat more quadrangular than ovate.

The enlarged third maxillipeds and the absence of a posterior arthrobranch at the base of the fourth pereiopod in the paratype align this crayfish with *Troglocambarus maclanei*; these are the only species assigned to the Cambarinae in which this gill has been observed to be lacking. As noted above, it is present in an exuvia of the holotype, so whether or not the absence of the gill is a unique feature of the paratypic female, the only specimen from which the branchiostegite was removed, needs to be confirmed.

The relationships of *P.* (*O.*) *delicatus* to other southeastern troglobitic crayfishes and their epigean relatives were discussed by Hobbs & Franz (1986) and the opinions expressed are equally applicable to *P.* (*O.*) *delicatus.* The previously known troglobites were treated in their review of the crayfishes of Florida by Franz & Franz (1990) and Hobbs & Hobbs (1991).

Etymology.—Attiguus (L.) = neighboring; alluding to the proximity of the type, and only known, localities of the new species and *P.* (*O.*) *delicatus* as well as to the close kinship of these crayfishes.

Acknowledgments

We are grateful to T. Morris for collecting the specimens that were made available to us for this study, for much of the data included in the description of the type locality, and for his maintaining the male in an aquarium until it had molted to first form. We also extend our thanks to J. F. Fitzpatrick, Jr., of the University of South Alabama, H. H. Hobbs III, of Wittenberg University, and T. E. Bowman, of the National Museum of Natural History, for their criticisms of the manuscript.

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A NEW GENUS OF PERISCELIDIDAE (DIPTERA) FROM THE NEOTROPICS

Wayne N. Mathis and László Papp

Abstract.—*Parascutops,* a new genus of the family Periscelididae (Diptera), is described, with *Scutops maculipennis* Malloch (Mexico) as its type species. Its relationships within the family Periscelididae and subfamily Periscelidinae are discussed, and diagnoses of the family-group taxa are also provided.

The family Periscelididae, better known in the older literature as Periscelidae, is comparatively new in the nomenclatural history of Diptera (Oldenberg 1914), and on a world basis the family has relatively few species. Fewer than 60 species have been described (Sabrosky 1965, Pires do Prado 1975, Papp 1984a), but more will undoubtedly be added, especially from the tropics (Amorim & Vasconcelos 1990). The purpose of this paper is to describe a new genus within the context of our concept of the family and subfamily Periscelidinae. The family-group taxa are also diagnosed herein, and appropriate keys to the included taxa are provided.

Even though the family has many more taxa than the number of described species now indicates, it is still small by hexapod standards. The small size of the family coupled with the relative scarcity of specimens in collections and the lack of any direct economic importance have resulted in a dearth of research on the family. A few genera have attracted some notice, however, largely because of their unusual natural histories. The genus *Periscelis* is best known because it breeds in fluxes associated with open wounds of deciduous trees (see Teskey 1976 for a review). Unfortunately the immature stages and natural history of the vast majority of species remain unknown.

Although the family is poorly known, the taxa included in it and its characterization have vacillated rather dramatically. Until recently, the family included only those genera here assigned to the subfamily Periscelidinae (Hennig 1969), and one of these (*Diopsosoma* Malloch) is now questionably associated. In this paper we adopt McAlpine's (1978, 1983) expanded concept of the family. McAlpine (1978, 1983) included a few genera that were previously assigned to the family Aulacigastridae, such as *Cyamops* Melander, *Planinasus* Cresson, and *Stenomicra* Coquillett. These genera are closely related and are here recognized as the subfamily Stenomicrinae. This subfamily has recently been given status at the familial level (Papp 1984b, Khoo & Sabrosky 1989), but we prefer recognition of it as a subfamily, as it is closely related to Periscelidinae. Although McAlpine's characterization of Periscelididae is adopted here, additional changes will undoubtedly be made to the concept of and taxa included in this family as other studies contribute to our understanding of the family.

Methods and Materials

All of the specimens for this study are from the National Museum of Natural History (USNM). The descriptive terminology, with the exceptions noted in Mathis (1986), follows that published in the Manual of Nearctic Diptera (McAlpine 1981). The descriptions are composite, not based solely on a genus or the holotype of a species.

Family Periscelididae Oldenberg, 1914

Periscelidinae Oldenberg, 1914:41.
Periscelidae.—Hendel, 1916:297.

Diagnosis.—Head: Frons with 1–2 fronto-orbital setae; postvertical setae present and divergent or absent (convergent in some *Stenomicra*). Pedicel cap-like and with a dorsal cleft, bearing 1 or more dorsoapical setae; 1st flagellomere frequently sharply deflexed, arising from ventral surface of pedicel; arista pectinate (sometimes bipectinate). Face uniformly sclerotized and arched, usually setose laterally (except in some *Cyamops*).

Thorax: Dorsocentral setae usually 2 (0+2), sometimes 1 (0+1), none presutural; posterior intra-alar seta reduced; scutellum with 1–2 pairs of marginal setae; scutellar disc bare; anepisternal seta usually lacking (present in *Planinasus* and some *Stenomicra*). Wing: subcosta rudimentary, not reaching costal margin, but not fused apically with R_1; no costal breaks (a weakness in the costa just apicad of the humeral crossvein in *Planinasus*; a definite narrowing, virtually amounting to a break at Sc in many *Stenomicra* and *Cyamops*); costa extended to vein R_{4+5} or M; cell dm with a fold running entire length; cell *cup* usually present, although CuA_2 either well developed or extremely reduced. Mid tibia bearing prominent, apicoventral seta.

Discussion.—The two subfamilies recognized in Periscelididae are easily distinguished from each other by the characters that are noted in the following key.

Key to Subfamilies of Periscelididae

1. Fronto-orbital seta 1; ocellar setae present. Costa short, extended to vein R_{4+5}; CuA_2 weak or lacking, thus lacking a cell cup; postpronotum bearing a well-developed seta .... Periscelidinae
– Fronto-orbital setae 2; ocellar setae absent. Costa long, extended to vein M; CuA_2 usually well developed, usually with a distinct cell cup (weak or lacking in *Stenomicra*); postpronotum lacking a well-developed seta (except in some *Stenomicra*) .... Stenomicrinae

Subfamily Periscelidinae Oldenberg, 1914

Periscelidinae Oldenberg, 1914:41.

Diagnosis.—Head: Eye microsetulose (sometimes sparsely so); occiput with a silvery white, microtomentose area immediately adjacent to posterior margin of compound eye; frons with 1 fronto-orbital seta only, reclinate; postvertical setae present, divergent; ocellar setae present, well developed; face uniformly sclerotized and transversely arched (shield-like in *Scutops*); face setose laterally, strongly receded ventrally, extended laterally below gena; gena extended anterodorsally, bearing a row of setae, with anterior one inserted well above oral margin; mouth opening large.

Thorax: Postpronotal seta well developed. Wing with costa extended to R_{4+5}; cell cup present, although CuA_2 extremely reduced.

Abdomen: 7th spiracle ("stigma") not free in female postabdomen. Postabdomen of male symmetrical; cerci usually narrowly fused dorsomedially, well sclerotized, much longer than wide; aedeagus very long, slender; aedeagal apodeme a somewhat flattened, mostly rectangular piece between base of aedeagus and hypandrium; ejaculatory apodeme well developed; gonites short, usually pointed, sheathing base of aedeagus; hypandrium shallowly concave to a deep pocket. See Griffiths (1972) for further discussion of the male terminalia.

Discussion.—The immature stages, and to an extent the adults, are associated with sap from bleeding deciduous trees (species of *Ulmus, Quercus,* and *Populus*). Teskey (1976) described and figured a larva of *Periscelis* sp.

The genera comprising Periscelidinae are those that Hennig (1969) included in his more restricted concept of the family, viz: *Periscelis, Marbenia* Malloch, *Neoscutops* Malloch, *Scutops* Coquillett, and the new genus that is described below. Hennig also included *Diopsosoma* Malloch, but its relationship with this family seems doubtful. The five included genera comprise a well-established, monophyletic assemblage, with corroborative synapomorphies as follows: 1. Mouth opening large. 2. Occiput with a silvery white, microtomentose area immediately adjacent to the posterior margin of the compound eye. 3. Only one fronto-orbital seta, reclinate. 4. Costal vein short, extended only to vein R_{4+5}. The generalized condition, found in related genera and families, is for the costal vein to extend to vein M. 5. Vein CuA_2 reduced or absent. Typically this vein is present, resulting in a well-defined cell cup. Its reduction or absence here is an autapomorphy. 6. Several characters of the male terminalia (see Griffiths 1972).

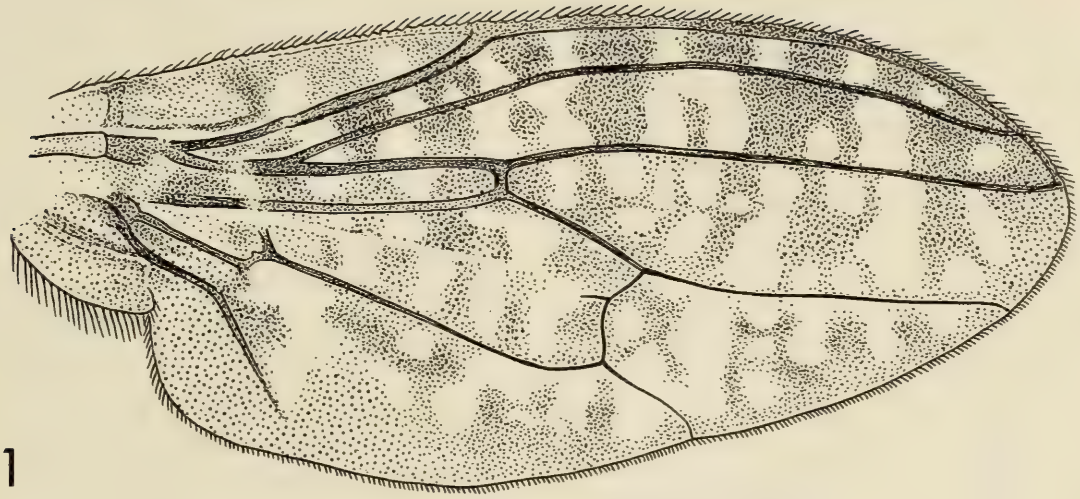
Key to Genera of the Subfamily Periscelidinae

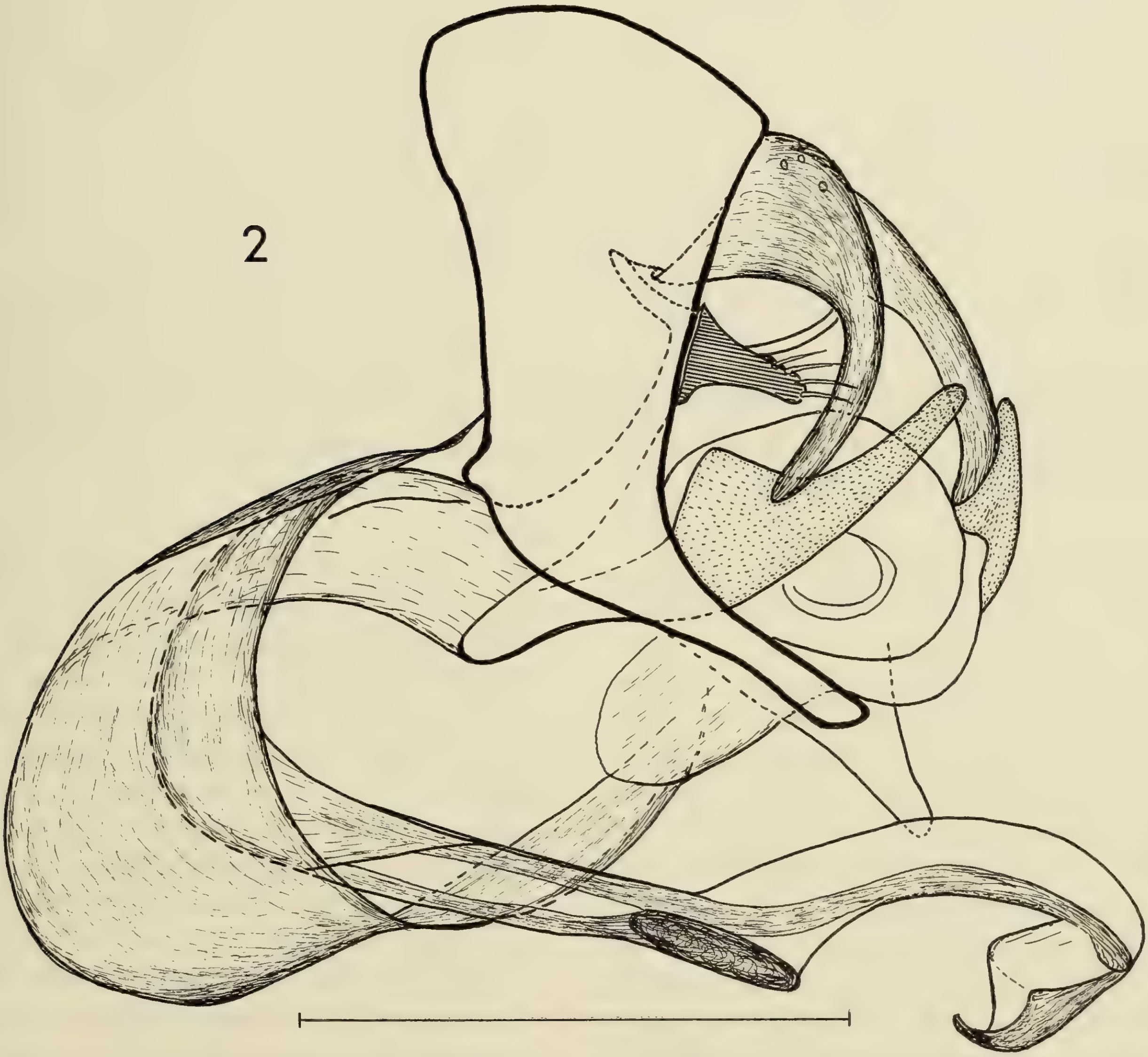
1. Eyes borne on conspicuous stalks; pedicel semiporrect. A presutural seta well developed; anepisternum setose; scutellum triangular, apex pointed and bearing apical patch of setae .... *Diopsosoma* Malloch
– Eyes not borne on conspicuous stalks; pedicel not porrect. Lacking a presutural seta; anepisternum bare of setae; scutellar apex usually broadly rounded to truncate (pointed in *Parascutops*), lacking apical patch of setae 2
2. Face vertically arched in lateral view, not distinctly angulate and dorsal surface of face not distinctly flattened, shield-like 3
– Face distinctly angulate in lateral view 4
3. Face smooth, lacking microtomentum, shiny. Wing generally infuscate, lacking pale areas; apical section of vein M usually conspicuously arched; vein R_{2+3} curved anteriorly toward costa to just beyond R_1, thereafter more or less evenly and shallowly arched, parallel to costa until merger with latter; vein R1 lacking setae on dorsal surface; only 1 posterior dorsocentral seta .... *Neoscutops* Malloch
– Face microtomentose, appearing dull, bearing 2 conspicuous transverse furrows. Wing infuscate on at least apical ½ and with a preapical, pale, transverse band; apical section of vein M straight or very shallowly arched; vein R_{2+3} more or less evenly arched throughout length except just before apex; vein R1 with dorsal surface setose; posterior dorsocentral setae 2 .... *Marbenia* Malloch
4. Dorsal area of face narrow, not distinctly flattened and shield-like. Wing generally hyaline, infuscation restricted to at most a transverse band .... *Periscelis* Loew
– Dorsal area of face broad, distinctly flattened, shield-like. Wing with at least apical ⅓ conspicuously infuscate 5
5. Wing mottled; mesonotum dull, densely microtomentose, mostly gray, with several brown spots; a pair of distinct prescutellar acrostichal setae. Arista with 3–4 dorsal branches ..... *Parascutops,* new genus
– Wing darkly infuscate on apical ½–⅓ and with subapical, transverse, white area or band; mesonotum very thinly microtomentose, subshiny to shiny; prescutellar acrostichal setae lacking. Arista with 7 or more dorsal branches .... *Scutops* Coquillett

Parascutops, new genus

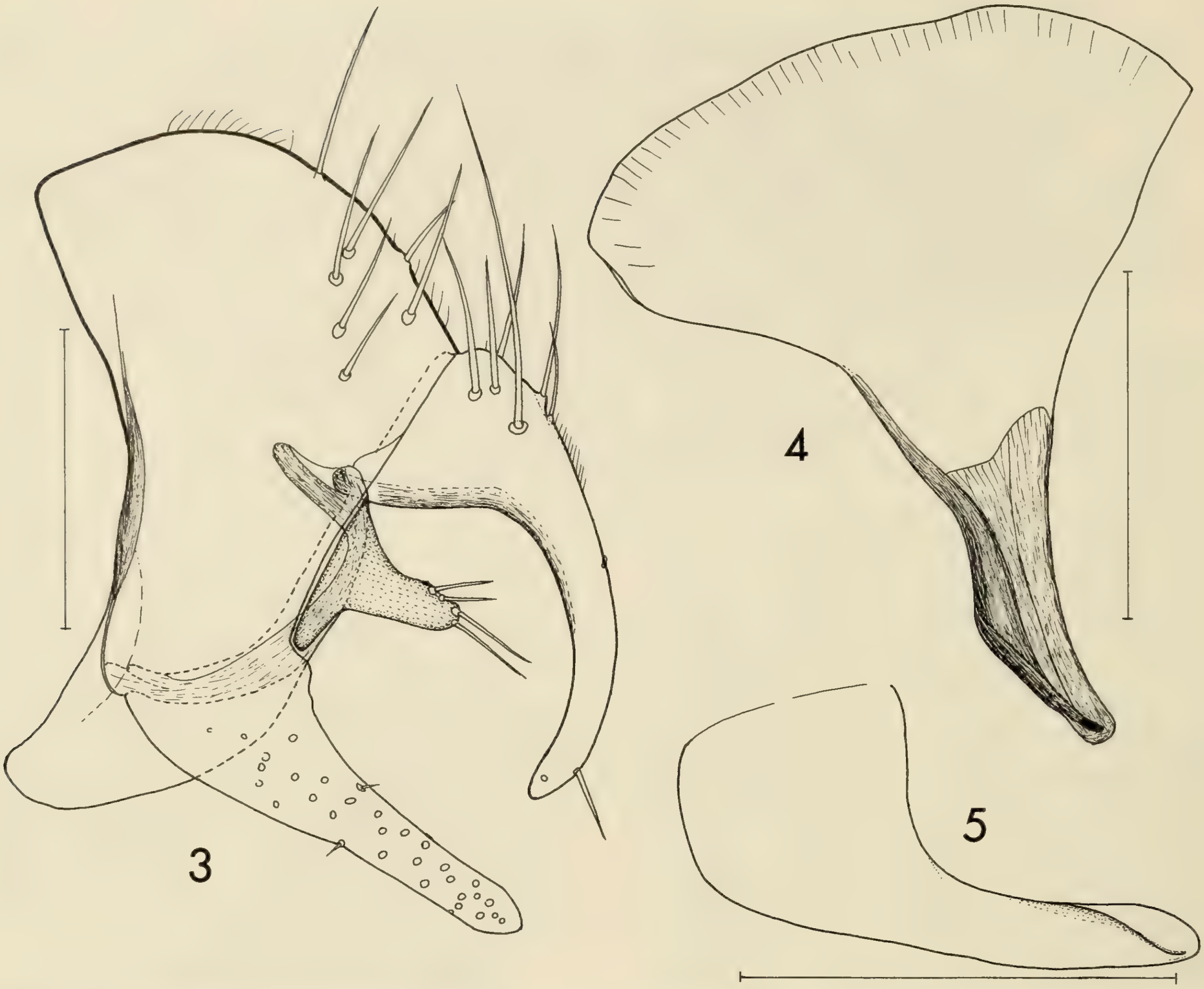
Type species.—Scutops maculipennis Malloch, 1926, by present designation.

Diagnosis.—Moderately small to medi-





Figs. 1–2. *Parascutops maculipennis* (Malloch): 1, Wing; 2, Male genitalia, sublateral-subventral view (cerci shaded, gonites dotted, epandrial process hatched, scale: 0.2 mm).



Figs. 3–5. *Parascutops maculipennis* (Malloch), male genitalia: 3, Epandrium and outer genital parts in a sublateral-subventral view, i.e., surstylus and cercus in widest extension (epandrial process dotted, most of the setulae on surstylus omitted; scale: 0.1 mm); 4, Ejaculatory apodeme in widest extension (scale: 0.2 mm); 5, Gonite (postgonite), lateral view (scale: 0.1 mm).

um-sized flies, body length 2.5 to 3.2 mm. Dorsum of head and thorax appearing dull, densely microtomentose.

Head: Face distinctly angulate in lateral view; dorsal half of face broad, distinctly flattened, shield-like, resembling species of *Scutops,* ventral half of face lacking transverse furrows. Arista with comparatively few branches dorsally and ventrally, 3–4; pedicel not porrect. Eyes not borne on conspicuous stalks.

Thorax: Mesonotal microtomentum mostly gray but with several brown spots; scutellum triangular, pointed posteriorly, lacking a patch of long setae apically. Chaetotaxy as follows: posterior dorsocentral setae 2; presutural seta lacking; prescutellar acrostichal setae well developed; anepisternum bare of setae. Basalar sclerite with an enlarged, anterior process that projects dorsally, apex bluntly rounded. Wing entirely mottled (Fig. 1); apical section of vein M straight or very shallowly arched; vein R1 bare above; vein R_{2+3} more or less evenly arched throughout length except just before apex; crossvein dm-cu arched to slightly angulate basally.

Abdomen: Male genitalia as follows (Figs. 2–5): Postabdomen completely symmetrical; epandrium narrowed dorsally, becoming wider ventrally and laterally, curved anteriorly; cerci strongly sclerotized, ventral ⅔ long, narrow, and parallel sided, in lateral view curved anteriorly (Fig. 3), bearing several long setae at base, otherwise setae sparse and short; genital pouch (hypandrium + aedeagal apodeme) small and rather flat, pocket-like (Fig. 2); epandrial process a short digitiform process between bases of cercus and surstylus, bearing setae apically (Figs. 2, 3), this epandrial process is completely apart from the lateral wall of epandrium but connected medially with structures under the epandrium; surstylus narrowly triangular (Figs. 2, 3), ventral ½ digitiform, ventral apex rounded, bearing numerous setulae along entire length; ejaculatory apodeme extremely large (compare scales of Fig. 3 and Fig. 4), distal portion widely triangular, proximal part ("hilt") strongly sclerotized; gonite (postgonite) caudally directed, comparatively long, with a flat, curved ridge subapically, apex rounded (Fig. 5); aedeagus long, thin, ribbon-like as in other genera of the subfamily but apical third with an extra strong curvature and apex with a small curved dentiform process (Fig. 2).

Discussion.—The only species now included in this genus, *maculipennis,* was described in the genus *Scutops,* and certainly the latter is closely related to *Parascutops.* Our study, however, especially of characters from the male terminalia, indicates a sister-group relationship with *Periscelis,* not *Scutops.* The ventrally oriented, slender process at the ventral margin of the epandrium between the surstylus and the cerci is apparently unique to these genera (this structure is secondarily lacking in species of the subgenus *Myodris* Lioy). Likewise the deeply concave genital pouch (hypandrium + aedeagal apodeme) that is semicircular in lateral view is a synapomorphy.

The conformation of the face, especially the flattened, shield-like portion, apparently developed independently in this genus and *Scutops.* Indeed, the shape of the face in *Parascutops* is somewhat intermediate between *Scutops* and *Periscelis.* Although the face of *Parascutops* is flattened and wide, as in *Scutops,* it differs from the latter in being broadly rounded ventrally, not pointed, and is similar in color to the frons, not white, as in *Scutops.*

Only the following species is now included in this genus.

Parascutops maculipennis (Malloch), new combination
Figs. 1–5

Scutops maculipennis Malloch, 1926:24 [Mexico. Mexico City; HT ♀, USNM (28458)].—Griffiths, 1972:120–123 [discussion], 282 [figs. of ♂ terminalia].—Pires do Prado, 1975:2 [neotropical catalog].

Distribution.—Neotropical: Mexico (Distrito Federal and Chapingo).

Natural History.—The specimens from Chapingo bear a label "in Casuarina," a tree that has been widely introduced throughout the tropical and temperate world from the Indopacific Region. Because periscelids are not known to be host specific, we suspect that the flies found on this tree were opportunistic and were not introduced along with the tree. An undescribed species of *Periscelis* is known from Australia, however (Colless & McAlpine 1974), and the possibility remains that this species also occurs there.

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MOLPADIID SEA CUCUMBERS OF CHINA, WITH DESCRIPTIONS OF FIVE NEW SPECIES (ECHINODERMATA: HOLOTHUROIDEA)

David L. Pawson and Yulin Liao

Abstract.—The molpadiid holothurian fauna of China is now known to comprise ten species, of which five, *Caudina atacta, C. zhejiangensis, Paracaudina delicata, Molpadia changi,* and *M. guangdongensis,* are described here as new.

The molpadiid holothurians of China are imperfectly known, and have never been studied as a group. Chang (1934), Chang & Liao (1964), and Liao (1984) recorded five species in their works on the holothurians of China. Over the past 35 years, the shallow coastal waters of China have been investigated by means of shore collecting and offshore benthic sampling. The resulting extensive collection of molpadiid holothurians forms the basis of this paper. In addition, the U.S. Fisheries Commission Steamer *Albatross* collected several molpadiids during its voyages to the Orient in 1907 and 1910.

Y.L. is grateful to the Short-Term Visitor program of the Office of Fellowships and Grants, Smithsonian Institution, which facilitated his study of the *Albatross* collections at the National Museum of Natural History (USNM), Smithsonian Institution, in March and April 1990.

Type specimens and other material are deposited at the USNM or at the Institute of Oceanology, Academia Sinica (IOAS), Qingdao, People's Republic of China.

Order MOLPADIIDA Haeckel, 1896

See Mortensen 1927:40; Pawson 1977:98; 1982:818.

Diagnosis.—Tentacles 15, digitate; body stout, lacking tube feet, usually with an evident tail; anal papillae, tentacle ampullae and respiratory trees present; ossicles may include tables, cups, fusiform rods or perforated plates, and modified anchors; phosphatic bodies often present.

Key to Families of Molpadiida known from China

1. Tentacles with a terminal digit and one to three pairs of lateral digits; tail usually evident; ossicles derived from triradiate tables and modified anchors, fusiform rods or perforated plates; phosphatic bodies usually present .... Molpadiidae
– Tentacles without a terminal digit and with one or two pairs of lateral digits; tail sometimes inconspicuous; ossicles large tables, crossed cups, perforated plates or irregular rods; phosphatic bodies usually absent .... Caudinidae

Family Molpadiidae Müller, 1850

See Heding, 1931:277; Pawson, 1977:98; 1982:818.

Diagnosis.—See key above.

Genus *Molpadia* Risso, 1826

See Pawson, 1977:99.

Diagnosis.—As for the family.

Key to Species of *Molpadia* from China

1. Anchors and racquet-shaped plates present ....*M. roretzi* (v. Marenzeller)
– Anchors and racquet-shaped plates absent 2
2. Discs of tables incomplete, three-

armed, each arm branching dichotomously; spires smooth, without teeth on pillars ....
.... *M. guangdongensis,* n. sp.

– Discs of tables complete, triangular to circular in outline, spires with two or three teeth on pillars ....
.... *M. changi,* n. sp.

Molpadia roretzi (v. Marenzeller)

Haplodactyla roretzi v. Marenzeller, 1877: 29, pl. 4, fig. 1.

Ankyroderma roretzi.—v. Marenzeller, 1881:124–126, pl. 4, fig. 4.—Théel, 1886: 49.—Mitsukuri, 1912:267, pl. 8, fig. 78, textfig. 55.

Ankyroderma simile Théel, 1886:40–41, pl. 2, fig. 5, pl. 11, fig. 2.

Molpadia similis.—H. L. Clark, 1907:163, pl. 10, fig. 6.

Molpadia roretzi.—H. L. Clark, 1907:163.—Ohshima, 1915:249.—Chang, 1934:23, textfigs. 11–12, pl. 3, fig. 1.—Chang & Liao, 1964:44.

Molpadia chinensis Chang, 1934:26, textfig. 13–14, pl. 3, fig. 2.

Material examined.—Numerous specimens from Yellow Sea, East China Sea and South China Sea, in depths of 44–200 m. In USNM, *Albatross* Station 5194, 11°15′N, 124°11′E, 271 m, 1 specimen.

Diagnosis.—Large to medium-sized, up to 120 mm long; phosphatic bodies abundant, imparting reddish brown or purple color to body wall; ossicles include anchors and racquet-shaped bodies, and scattered tables of varying shape, usually with a circular disc, 60–70 μm in diameter.

Remarks.—This is apparently the most common *Molpadia* in China, especially in the Yellow Sea and East China Sea. There are over 100 specimens in the IOAS, collected at various stations from the Yellow Sea to the South China Sea in 44–200 m depth. They are 20–100 mm long, with great variation in number and form of the phosphatic bodies and ossicles, and color of body wall. The smallest specimens are gray, and yellowish-brown dots indicating developing phosphatic bodies are visible only under the microscope. In full-grown specimens, the phosphatic deposits are aggregated; thus, the body wall is dark brown to dark purple.

All of the 17 specimens from the South China Sea in depths of 145–200 m are small, 20–30 mm long; the phosphatic bodies are scarce, and yellowish in color.

Molpadia chinensis (Chang 1934) was based upon two specimens that are sympatric with *M. roretzi.* The morphology and body wall ossicles of *M. chinensis* fall within the range of variation of *M. roretzi,* and we believe these species are synonymous.

Distribution.—From southern Japan to the South China Sea, southward to the Philippines, in 44–620 m.

Molpadia changi, new species
Fig. 1

Molpadia andamanensis.—Chang & Liao, 1964:45 [Not *M. andamanensis* (Walsh)].

Material examined.—Ninety six specimens. Holotype: IOAS E1007, off Zhejiang Province, 29°N, 122°30′E, 9 Jul 1959, 53 m, muddy bottom. Paratypes: IOAS E1008, same locality as Holotype, 3 specimens; USNM E40415, same locality as Holotype, 3 specimens; IOAS E1010, 33°N, 124°E, 66 m, 2 specimens; IOAS E1011, 29°N, 123°E, 63 m, 5 specimens; IOAS E1012, 29°N, 123°30′E, 81 m, 27 specimens; IOAS E1013, 29°30′N, 123°30′E, 63 m, 1 specimen; IOAS E1014, 29°30′N, 124°E, 69 m, 3 specimens; IOAS E1015, 28°30′N, 122°30′E, 63 m, 10 specimens; IOAS E1016, 28°30′N, 123°30′E, 85 m, 4 specimens; IOAS E1017, 28°30′N, 124°E, 90 m, 1 specimen; IOAS E1018, 29°30′N, 122°45′E, 50 m, 2 specimens; IOAS E1019, 21°45′N, 113°45′E, 35 m, 1 specimen; IOAS E1020, 21°45′N, 114°E, 38 m, 7 specimens; IOAS E1021, 21°N, 112°E, 45 m, 7 specimens; IOAS E1022, 21°N, 113°30′E, 42 m, 7 specimens; IOAS E1023, 20°45′N, 111°30′E, 47 m, 4 specimens; IOAS

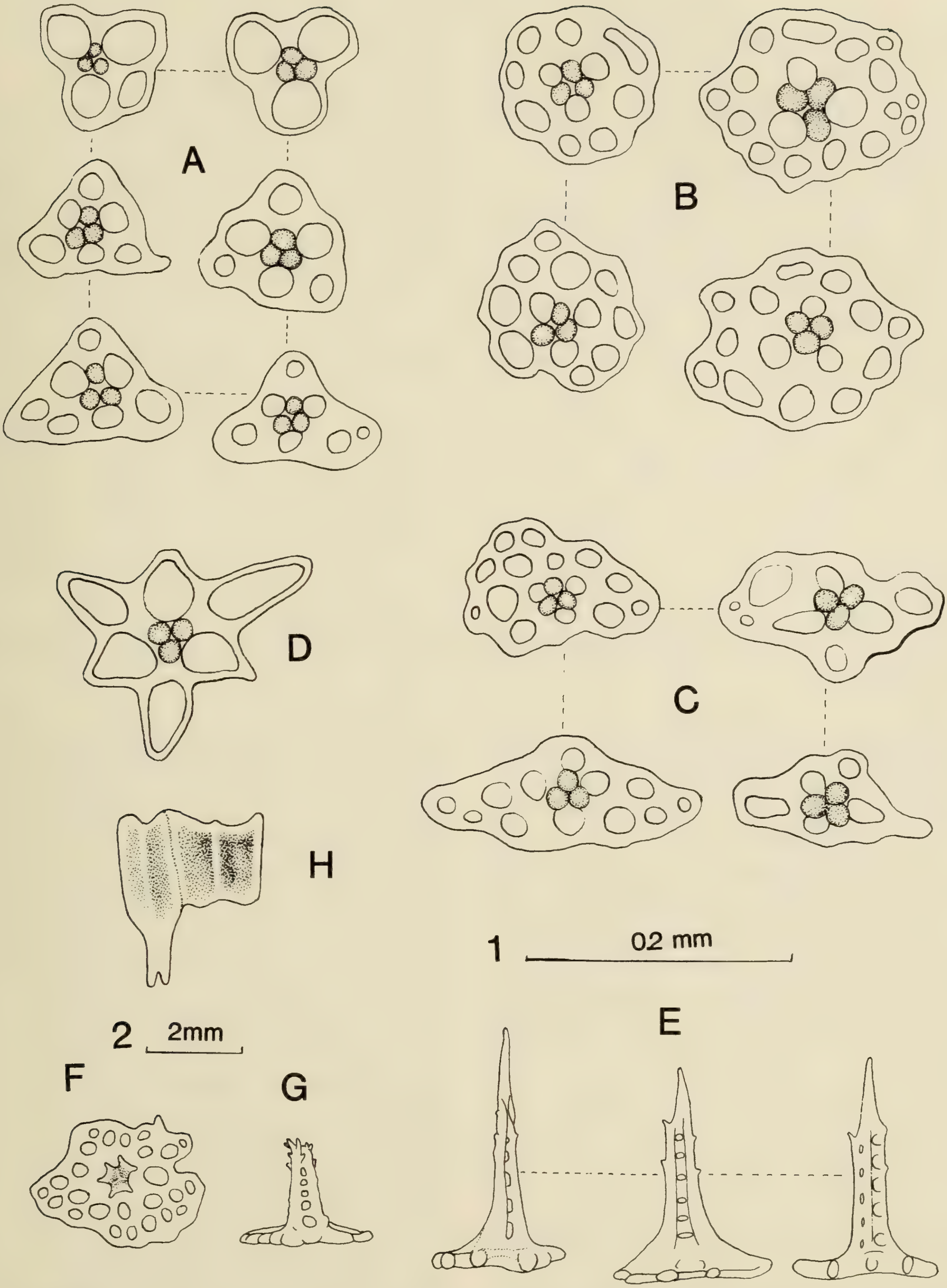

Fig. 1. *Molpadia changi,* new species. A, triangular tables from body wall; B, circular tables from body wall; C, elongate oval tables from body wall; D, delicate table from body wall; E, body wall tables in profile; F, table from tail; G, table from tail in profile; H, radial and interradial pieces of calcareous ring.

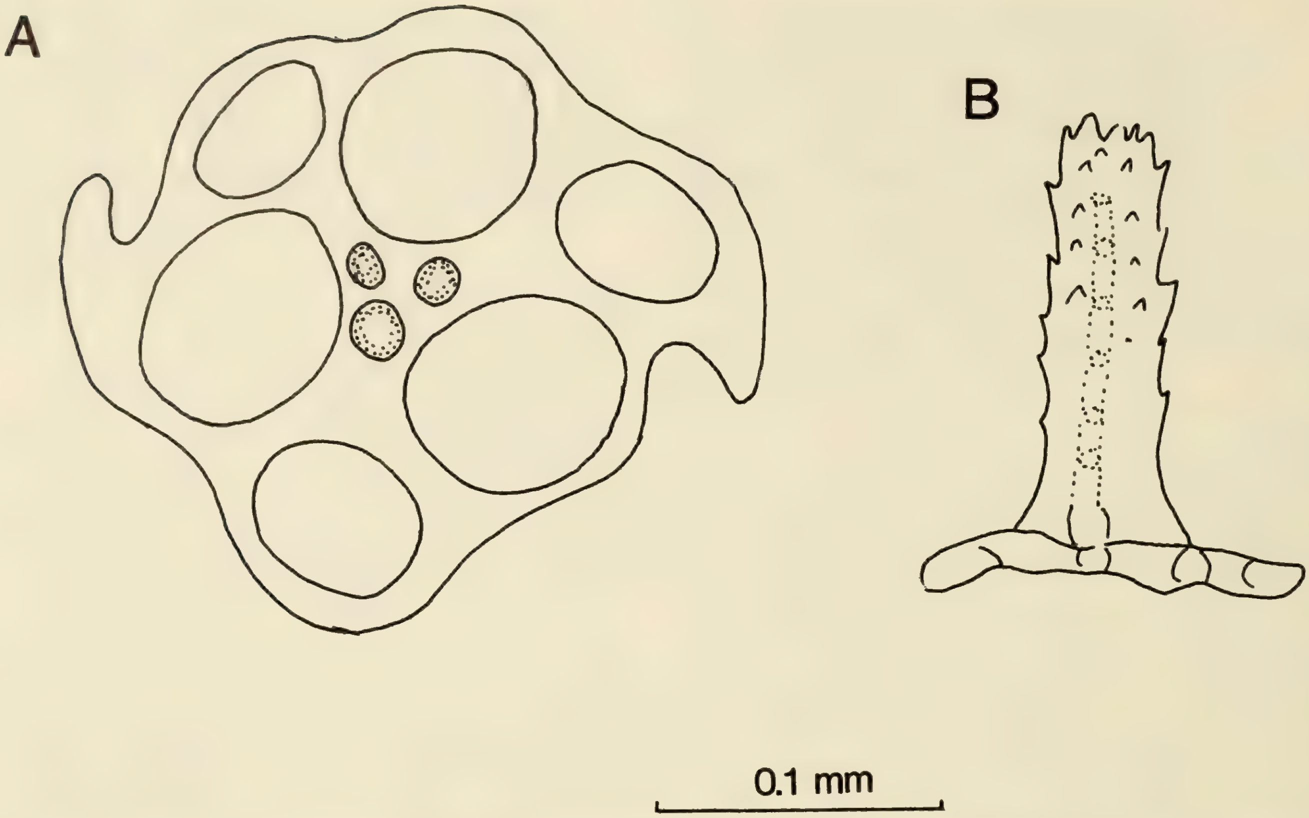

Fig. 2. *Molpadia andamanensis* (Walsh) from Indian Ocean. A, table from body wall; B, table from body wall in profile.

E1024, 22°N, 114°30′E, 46 m, 4 specimens; IOAS E1025, 21°45′N, 112°30′E, 41 m, 4 specimens; IOAS E1026, 20°N, 111°45′E, 44 m, 1 specimen.

Diagnosis.—Medium-sized to large, largest specimen 120 mm long. Phosphatic bodies present. Ossicles in body wall and tail exclusively tables, the discs circular to triangular, with undulating margin and 3–16 perforations; spires high, composed of three pillars joined by 5 or 6 crossbars, pillars fused distally to form a single point. Outer surface of spire carries 2 or 3 teeth.

Description.—Holotype total length 85 mm, diameter 28 mm, tail 20 mm; largest Paratype 120 mm long, 48 mm diameter. Body of typical molpadiid shape. Tentacles with a pair of minute digits. Anus surrounded by 5 groups of minute papillae. Body wall thin, delicate, slightly rough to touch. Calcareous ring with sculptured surface; radial pieces with short bifurcate posterior projections (Fig. 1H). Stone canal and Polian vesicle single. Color in alcohol light brown, tail whitish.

Ossicles exclusively tables (Fig. 1A–E), discs 100–160 μm in diameter, circular to triangular in outline, with undulating margin; 3–16 perforations in disc. Spires high (averaging 160 μm), composed of 3 pillars joined by 5 or 6 crossbars; pillars fuse distally to form a single projection. Outer surface of spire carries 2 or 3 teeth. More delicate tables, averaging 150 μm in diameter, often with approximately 6 perforations, are also scattered in the body wall. Phosphatic deposits present, scattered. Tail with tables (Fig. 1F, G) lower and smaller than those described above; disc with numerous small perforations, and short spires with several terminal teeth.

Remarks.—This new species has been confused with *Molpadia andamanensis* (Walsh), an East Indies and Indian Ocean species with a bathymetric range of 310–1210 m. Chang & Liao (1964) reported *M. andamanensis* from 35–90 m off China, but this material was, in fact, *M. changi.* Examination of specimens of *M. andamanensis* in the USNM enables us to confirm that

Chinese specimens do indeed represent a different species. In *M. changi,* the tables are 100–160 μm in diameter, with spires terminating in a single point, while in *M. andamanensis* the tables are 200–280 μm in diameter, with spires terminating in numerous teeth (Fig. 2A–B).

Distribution.—From the Yellow Sea (33°N, 124°E) to the Philippines (11°38′N, 124°40′E), in 35–90 m.

Molpadia guangdongensis, new species
Fig. 3

Material examined.—Twenty six specimens. Holotype: IOAS E1009, off the east coast of Hainan Island, 19°N, 111°30′E, 19 Oct 1959, 144 m. Paratypes: IOAS E1027, same locality as Holotype, 3 specimens; IOAS E1028, 17°45′N, 110°30′E, 200 m, 5 specimens; IOAS E1029, 18°N, 110°30′E, 000 m, 3 specimens; IOAS E1030, 22°116′E, 89 m, 1 specimen; IOAS E1031, 18°45′N, 111°E, 122 m, 1 specimen; IOAS E1032, 17°30′N, 110°E, 140 m, 3 specimens; IOAS E1033, 21°45′N, 115°30′E, 105 m, 3 specimens; IOAS E1034, 18°15′N, 110°30′E, 125 m, 1 specimen; IOAS E1035, 17°N, 109°30′E, 121 m, 1 specimen; IOAS E1036, 17°N, 109°30′E, 115 m, 1 specimen; IOAS E1037, 18°30′N, 111°E, 151 m, 1 specimen; USNM E40417, *Albatross* Sta. 5308, 21°54′N, 115°42′E, 113 m, 2 specimens.

Diagnosis.—Small form, 30–40 mm long. Phosphatic bodies absent, but outer body wall may be discolored. Ossicles exclusively tables with high smooth spires composed of 3 pillars joined by 8–9 crossbars; the pillars fused distally to form a single point. Discs of tables variable in shape, usually incomplete, with three dichotomised arms; disc may be complete, triangular, oval to irregular in outline, with 2–6 perforations.

Description.—Holotype total length 40 mm, diameter 15 mm, tail 3 mm. Body barrel-shaped, with very short tail. Calcareous ring with sculptured surface; radial pieces with short bifurcate posterior projections (Fig. 3H). Anus surrounded by 5 groups of papillae. Stone canal and Polian vesicle single. Body wall thin and rough to touch, due to presence of numerous ossicles with long spires. Color in alcohol grayish-white.

Ossicles exclusively tables (Fig. 3A–E) with high (averaging 200 μm) smooth spires composed of 3 pillars joined by 8–9 crossbars; distally the 3 pillars fuse to form a single projection, which rarely carries 2 or 3 recurved spines. Discs of tables 120–260 μm in diameter, greatly variable in shape, usually composed of three dichotomously branched arms, with extremities of the arms straight or only slightly curved. Sometimes table discs complete, oval to triangular, with 2–6 perforations. Tables in tail (Fig. 3F, G) fusiform rods, 220–270 μm long, with low spires and four central perforations.

Remarks.—This new species resembles *Trochostoma parvulum* Cherbonnier & Feral, 1981, from the Philippines, but it differs in that the 6 branches of the three-armed tables are not strongly curved; also, the distal extremities of the spires are fused to form a single point. Further, in their description of *T. parvulum,* Cherbonnier & Feral mention "Les uns, tres nombreux, caracteristiques de l'espece sont en forme d'un X dont les branches ont les extremites condees (fig. 28,A)." We have found no such X-shaped bodies in *Molpadia guangdongensis.*

Distribution.—South China Sea, from 17°N, 109°30′E, to 22°N, 116°E, in 89–200 m.

Family Caudinidae Heding, 1931

See Heding, 1931:282; Pawson, 1977:119; 1982:818.

Diagnosis.—See key above.

Key to genera of Family Caudinidae from China

1. Tentacles with 2 pairs of lateral digits; tail usually long and slender 2
– Tentacles without digits or with only

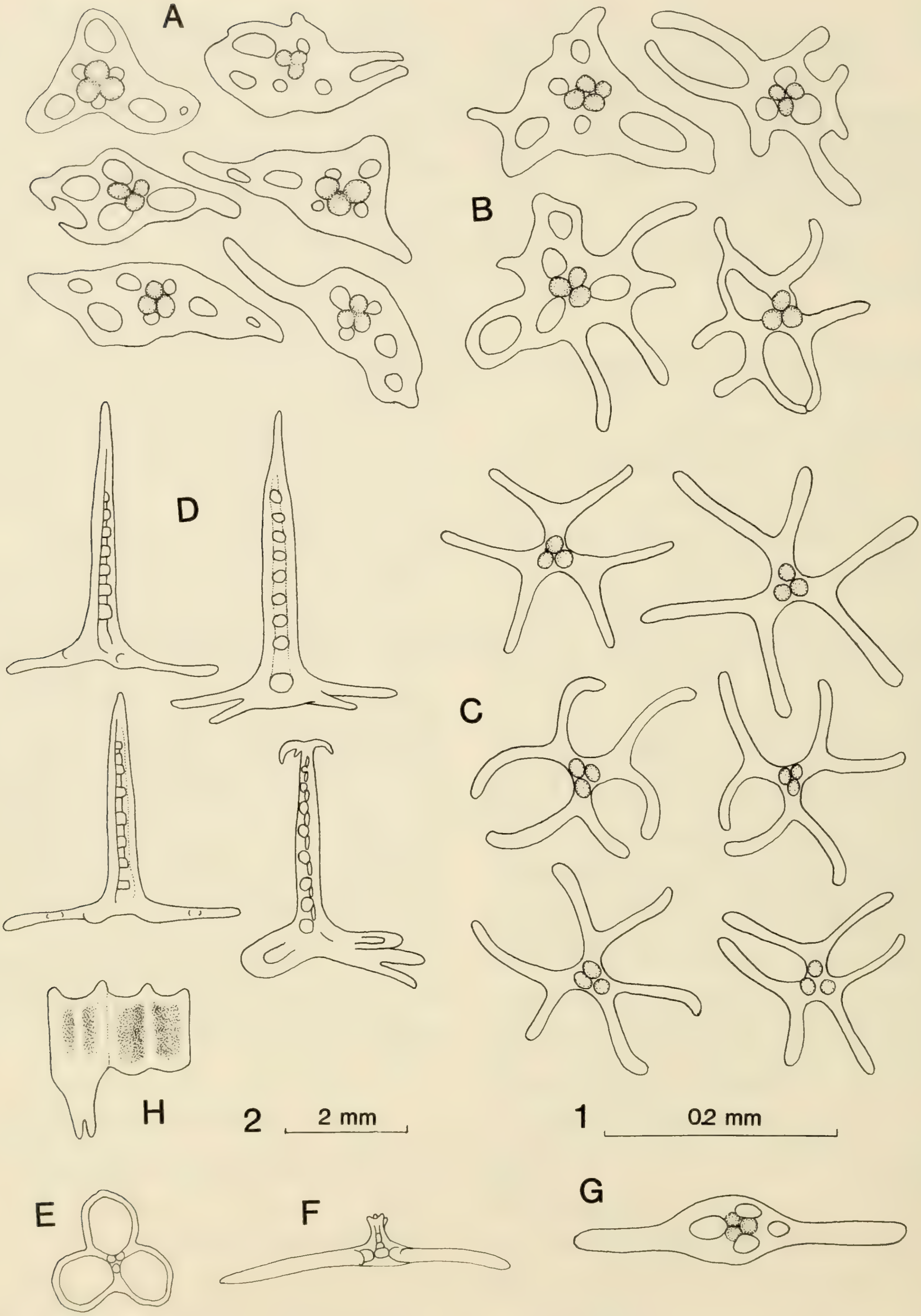

Fig. 3. *Molpadia guangdongensis,* new species. Elongate and rhomboid tables from body wall; B, irregular tables from body wall; C, tables from body wall with disc composed of 3 bifurcate arms; D, tables from body wall in profile; E, delicate table from body wall; F, table from tail in profile; G, table from tail; H, radial and interradial pieces of calcareous ring.

one pair of lateral digits; tail absent or inconspicuous .... *Acaudina*
2. Ossicles small cups, perforated plates, or irregular rods .. *Paracaudina*
– Ossicles large tables, and knobbed buttons or perforated plates .. *Caudina*

Genus *Caudina* Stimpson, 1853

See Deichmann, 1938:112; 1940:211.

Diagnosis.—Tentacles with 2 pairs of digits, the distal pair longer, but no terminal digit. Body barrel-shaped with a short or long tail. Radial pieces of calcareous ring with short posterior projections. Ossicles large tables, usually with a spire of 4 short pillars, terminating in a few teeth; knobbed buttons or irregular perforated plates also present.

Key to known species of *Caudina*

1. Tables inconspicuous, scarce, reduced to rods or plates, or lacking .... *arenicola* (Stimpson, 1853)
– Tables conspicuous, numerous, with well-developed spire and disk 2
2. Tables accompanied by knobbed buttons 3
– Tables accompanied by perforated plates 4
3. Buttons not abundant, weakly knobbed, usually oval in outline, with two large elliptical and two small circular holes .... *arenata* Gould, 1841
– Buttons abundant, strongly knobbed, usually with irregular outline, the four holes more or less alike in size and form .... *similis* (Augustin, 1908)
4. Discs of tables 180–280 μm in diameter; perforated plates very variable in form and in number of holes, lacking knobs .... *atacta,* n. sp.
– Discs of tables 150–180 μm in diameter; perforated plates vary only slightly in form and in number of holes, often possessing a few low knobs .... *zhejiangensis,* n. sp.

Caudina similis (Augustin)
Fig. 4

Trochostoma simile Augustin, 1908:38, pl. 2, fig. 7, textfig. 25.
Caudina similis.—Heding, 1931:283.—H. L. Clark, 1935:278.—Deichmann, 1938: 112.

Material examined.—Twenty specimens. IOAS E1038, 33°N, 123°E, 36 m, 1 specimen; IOAS E1039, 33°15′N, 123°30′E, 46 m, 1 specimen; IOAS E1040, 33°N, 124°E, 66 m, 15 specimens; IOAS E1041, 33°30′N, 123°E, 48 m, 3 specimens.

Diagnosis.—Medium-sized form up to 60 mm long; ossicles well-developed tables, discs circular to square with undulated margin and 10–16 holes arranged around a central opening, the spires of moderate height, solid, ending in 3 or 4 spines. Buttons regular or irregular in outline, strongly knobbed, with a varying number of holes.

Description.—Total length 40–60 mm, diameter 13–15 mm, tail about 30% of body length. Body fusiform, gradually tapering posteriorly into a narrow tail. Stone canal and Polian vesicle single. Radial pieces of calcareous ring with a short bifid posterior projection (Fig. 4G). Body wall firm, coriaceous, rough to touch. Color in alcohol yellowish-white.

Ossicles closely crowded tables and buttons. Tables (Fig. 4A, B) with circular to square discs 80–130 μm in diameter, slightly undulating margin, with 10–16 perforations surrounding a central opening; spires moderate, 60–80 μm high, solid, ending in four spines. Buttons (Fig. 4C, D) regular (80–90 μm long, 60–70 μm wide) to irregular (80–120 μm in diameter) in outline, strongly knobbed, with varying number of holes. In tail, tables (Fig. 4E, F) smaller, with distinct knobs on discs.

Remarks.—This species was based (Augustin 1908) on 4 specimens from southern Japan in 100–300 m, and apparently it has not been collected since. Study of material of *Caudina arenata* (Gould) in the USNM

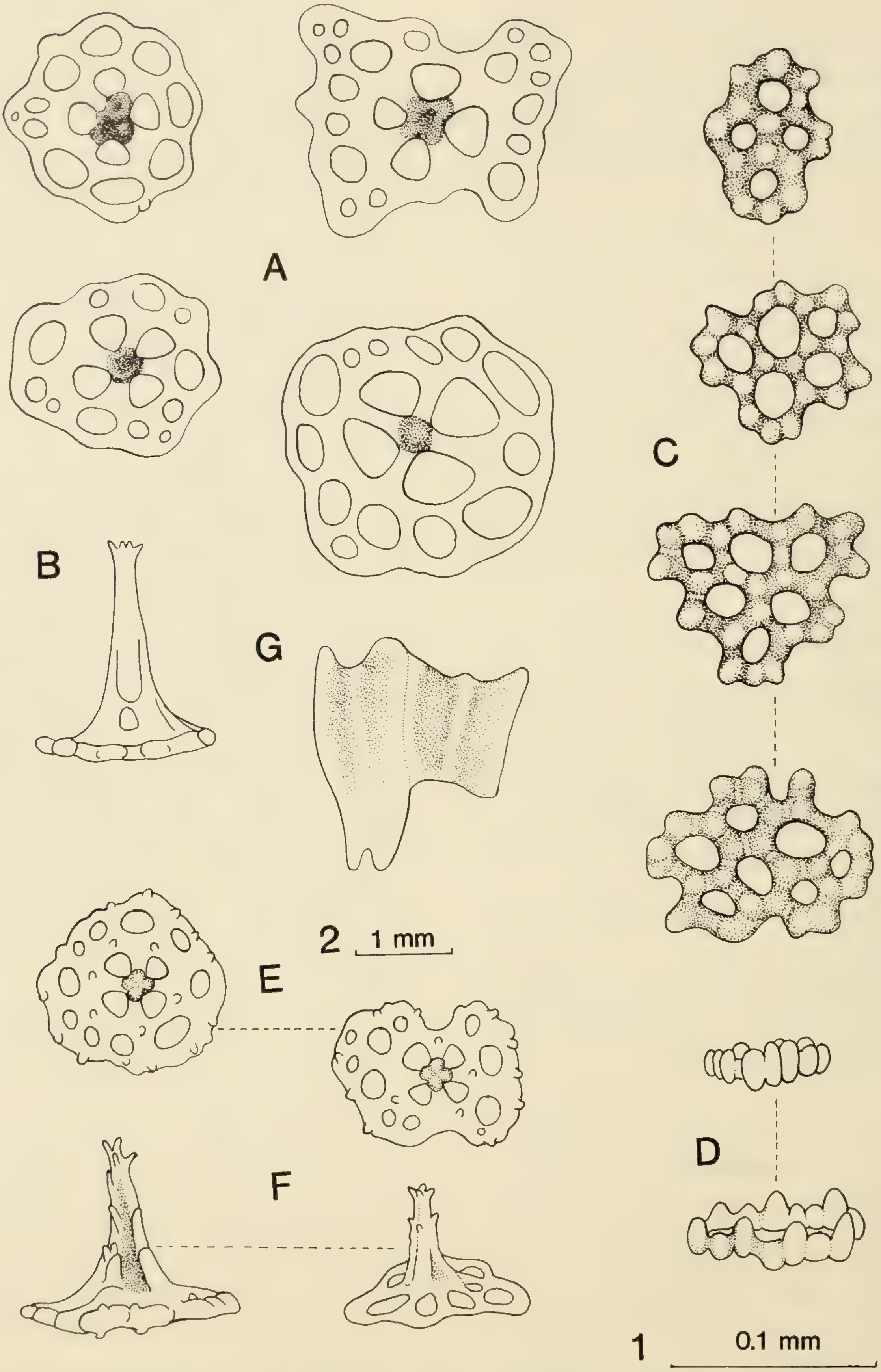

Fig. 4. *Caudina similis* (Augustin). A, tables from body wall; B, table from body wall in profile; C, irregular knobbed buttons; D, knobbed buttons in profile; E, tables from tail; F, tables from tail in profile; G, radial and interradial pieces of calcareous ring.

shows that these two species are undoubtedly closely related.

Distribution.—Known only from Sagami Bay, Japan, and the Yellow Sea, China, in 36–300 m.

Caudina atacta, new species
Fig. 5

Material examined.—Ten specimens. Holotype: IOAS E1005, Gulf of Tonkin, 17°45′N, 107°45′E, 13 Feb 1960, 80 m. Paratypes: IOAS E1042, same locality as Holotype, 2 specimens; USNM E40418, same locality as Holotype, 1 specimen; IOAS E1043, 18°30′N, 108°30′E, 63 m, 2 specimens; IOAS E1044, 19°N, 108°E, 73 m, 1 specimen; IOAS E1045, 18°30′N, 108°E, 69 m, 1 specimen; IOAS E1046, 18°30′N, 107°30′E, 72 m, 1 specimen; IOAS E1047, 17°30′N, 107°30′E, 91 m, 1 specimen.

Diagnosis.—Small form, largest 53 mm long. Ossicles large and stout tables, discs irregular in outline, with varying number of perforations; spires four-pillared, of low to moderate height, ending in 3 blunt teeth or in a single blunt point. Numerous perforated plates also present, with varying number of perforations, and frequently with one or more handle-like marginal projections.

Description.—Total length of Holotype 53 mm, diameter 20 mm, tail 24 mm long. Body barrel-shaped, with long and narrow tail. Anus not distinctly papillate. Body wall thick and rough to touch, due to presence of numerous ossicles. Short posterior projections on radial pieces of calcareous ring (Fig. 5F). Stone canal and Polian vesicle single. Color in alcohol whitish.

Ossicles numerous large and stout tables (Fig. 5A–C) 180–280 μm in diameter, discs thick, very variable in outline, with varying number of perforations. Spires low, 80–100 μm high, four-pillared, ending in 3 blunt teeth or in a single solid point. Plates (Fig. 5D) very numerous 160–220 μm long and 80–180 μm wide, very variable in shape and in number of perforations, usually with handle-like projection on margin. Tail with smaller tables (Fig. 5E), with more numerous perforations and with edge of disc slightly knobbed. No phosphatic bodies.

Remarks.—According to Deichmann (1938), members of the genus *Caudina* in the strict sense are *C. arenata* Gould from the eastern United States, *C. similis* (Augustin) from Japan, and *C. arenicola* (Stimpson) from southern California. *Caudina atacta* differs from the first two species in lacking knobbed buttons from the body wall, and *C. arenicola* usually lacks body wall ossicles, or they are reduced to rods and small plates.

Distribution.—Known only from the Gulf of Tonkin, ranging from 17°30′N, 107°30′E to 19°N, 108°E, in 63–91 m.

Caudina zhejiangensis, new species
Fig. 6

Material examined.—Twenty five specimens. Holotype: IOAS E1006, off Zhejiang Province, East China Sea, 29°N, 123°E, 3 Apr 1959, 65 m, muddy bottom. Paratypes: IOAS E1048, same locality as Holotype, 3 specimens; USNM E42003, same locality as Holotype, 9 July 1959, 68 m, 4 specimens; IOAS E1049, 29°30′N, 123°30′E, 53 m, 4 specimens; IOAS E1050, 29°30′N, 123°E, 61 m, 1 specimen; IOAS E1051, 28°30′N, 123°E, 78 m, 1 specimen; IOAS E1052, 28°30′N, 124°E, 89 m, 2 specimens; IOAS E1053, 28°30′N, 122°30′E, 63 m, 1 specimen; IOAS E1054, 28°N, 122°30′E, 79 m, 1 specimen; IOAS E1055, vicinity of Zhou-Shan Archipelago, 60 m, 8 specimens.

Diagnosis.—Small form up to 35 mm long. Numerous ossicles in form of tables, with circular to square discs; central hole surrounded by a simple single or double ring of 8 or 16 perforations; spires four-pillared, ending in three short teeth or a single conical projection. Numerous irregular perforated plates also present, usually with 4–12 perforations, and a few low knobs. Tail with

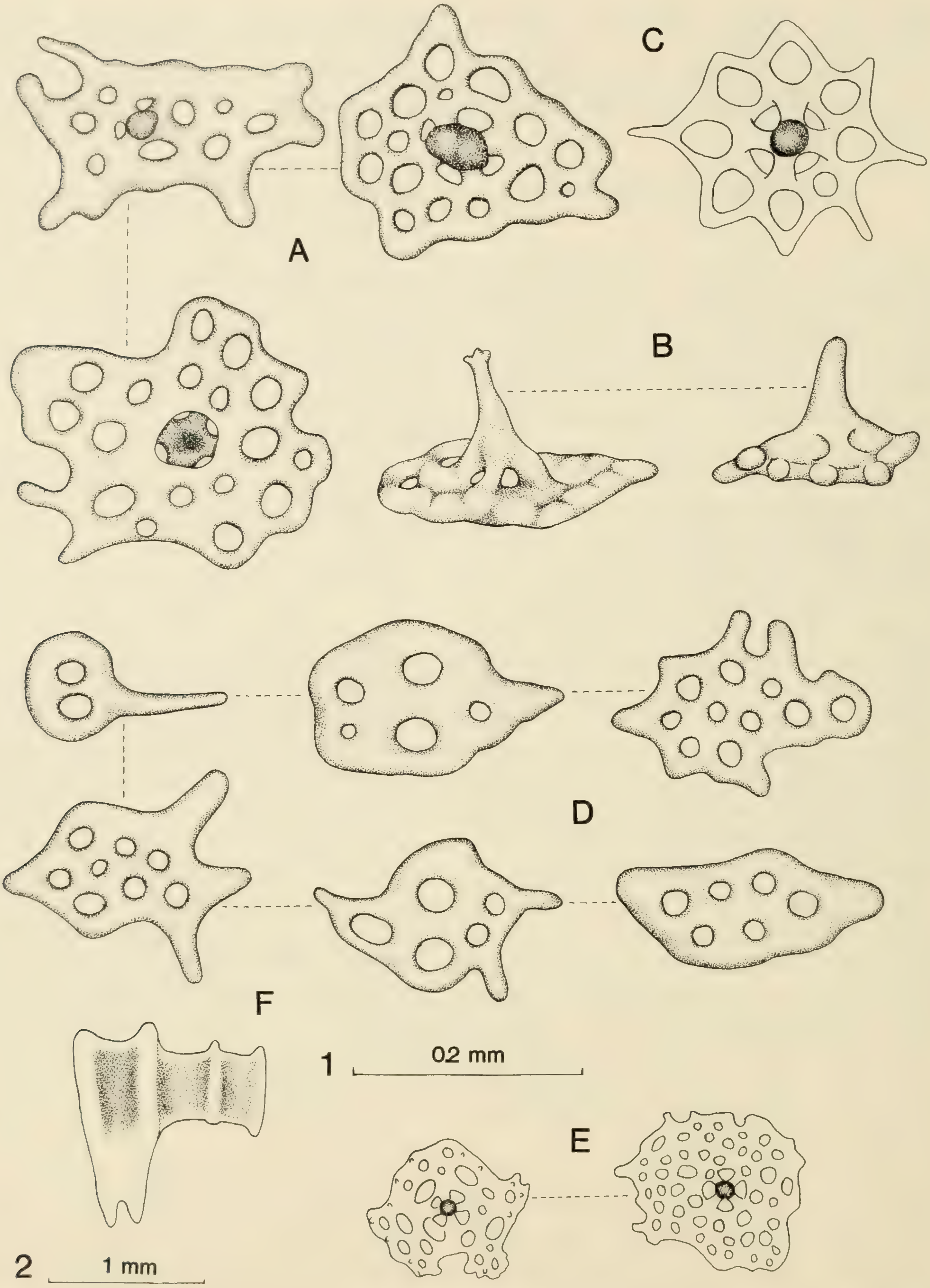

Fig. 5. *Caudina atacta,* new species. A, tables from body wall; B, tables from body wall in profile; C, delicate table from body wall; D, plates from body wall; E, tables from tail; F, radial and interradial pieces of the calcareous ring.

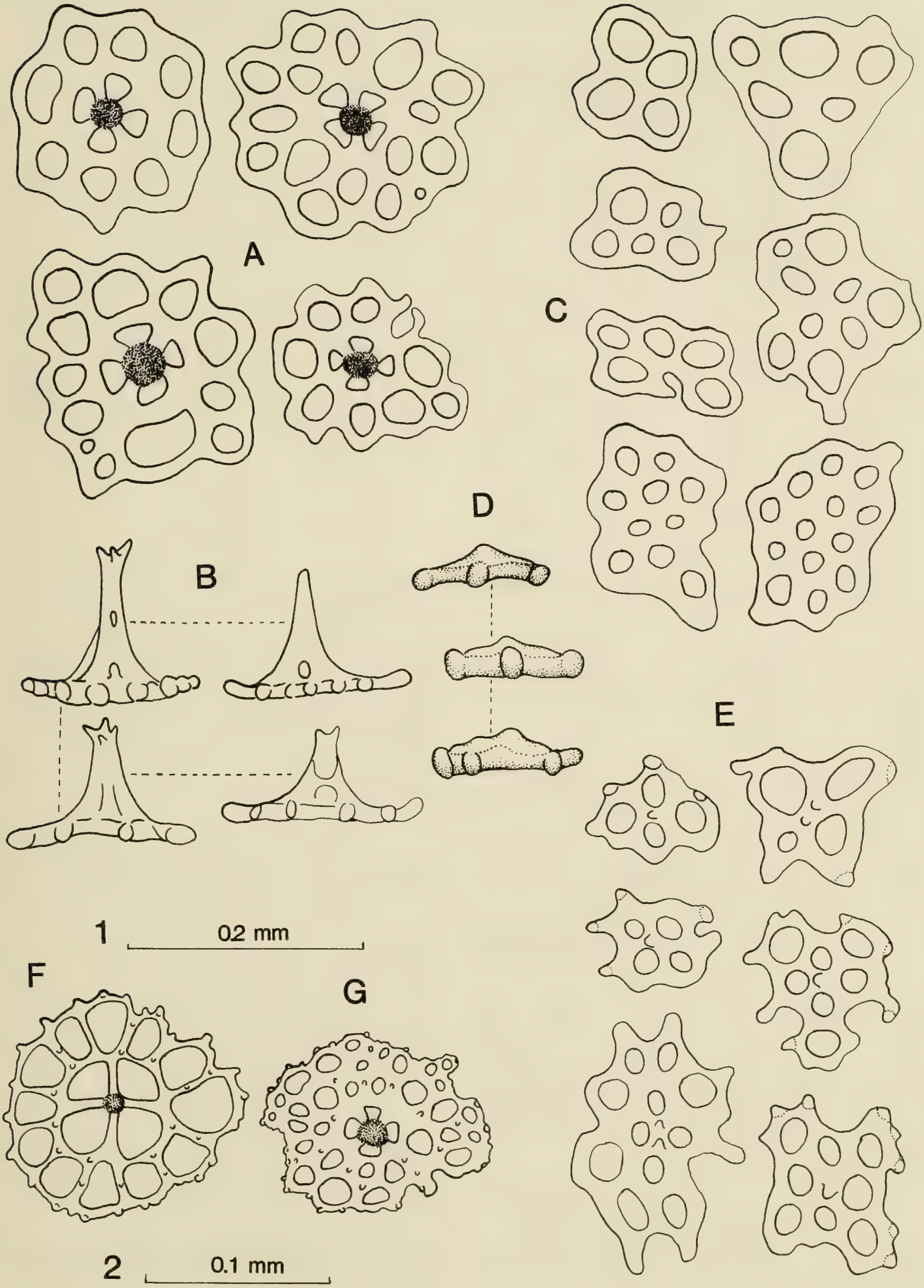

Fig. 6. *Caudina zhejiangensis,* new species. A, tables from body wall; B, tables from body wall in profile; C, irregularly perforated plates from body wall; D, knobbed perforated plates from body wall in profile view; E, knobbed perforated plates from body wall; F, delicate table from body wall; G, table from tail.

smaller tables, with numerous minute knobs along edge of the disc.

Description.—Holotype 35 mm long, 15 mm in diameter, tail 15 mm long. Body fusiform, tail long and slender. Anus surrounded by 5 minute projections. Stone canal and Polian vesicle single. Body wall coriaceous to translucent, rough to touch. Color in alcohol yellowish to whitish.

Ossicles numerous well-developed tables (Fig. 6A, B), discs circular to square in outline, 150–180 μm in diameter, with large central hole surrounded by a single ring of 8 perforations, or a double ring. Spire moderate, 80–100 μm high, four-pillared, ending in 3 short teeth or tapering to a point. Irregular perforated plates (Fig. 6C–E) 130–180 μm long, and 80–180 μm wide, with 4–12 large holes and sometimes some low knobs also present. Occasionally delicate tables (Fig. 6F) with some minute knobs on the disc can be found. No phosphatic bodies. Tables in tail (Fig. 6G) smaller, with numerous perforations and small knobs on periphery and elsewhere on the disc.

Remarks.—This species seems most closely related to *Caudina atacta,* described above, but it differs in having smaller and more regular tables, perforated plates with knobs, and occasional delicate tables with knobbed discs. The tables in the tail of *C. zhejiangensis* have more numerous knobs than those of *C. atacta.* As only a few echinoderm species are common to both the Gulf of Tonkin and off Zhejiang Province, it seems most reasonable to us to regard *atacta* and *zhejiangensis* as distinct species.

Distribution.—Known only from the East China Sea, in 53–89 m.

Genus *Paracaudina* Heding, 1931

See Heding, 1931:283; 1932:455; Pawson, 1977:119.

Diagnosis.—Tentacles 15, each with 2 pairs of digits; tail usually long and slender; ossicles small crossed cups, or perforated plates, or irregular rods; no phosphatic bodies, but a diffuse reddish to brownish pigment may occur in older individuals.

Key to species of *Paracaudina* known from China

1. Crossed cups distinctly delicate, with large perforations and fine cross-bridge and edge; margin of cups with fine finger-like projections .... *delicata,* n. sp.
– Crossed cups not delicate, but stout and thick, with small perforations and stout cross-bridge and edge; margin of cups with low and rounded projections .... *chilensis* (Müller, 1850)

Paracaudina delicata, new species
Fig. 7

Material examined.—Holotype: IOAS E1004, Gulf of Tonkin, 20°45′N, 109°15′E, 14 Nov 1959, 21 m, muddy bottom.

Diagnosis.—Ossicles delicate crossed cups with large perforations and fine cross-bridge and edge; knobs on cup surface prominent but small; margin of cups with fine finger-like projections.

Description.—Holotype 30 mm long, diameter 13 mm, tail about 8 mm long. Body barrel-shaped, with narrow tail. Body wall thin, more or less translucent, so that radial longitudinal muscles can be seen from outside. Radial pieces of calcareous ring with short bifid projections (Fig. 7D). Anus with five groups of papillae. No phosphatic bodies. Color in alcohol yellowish.

Body wall ossicles more or less numerous, in form of delicate crossed cups (Fig. 7A) 50–60 μm in diameter, with large perforations and fine cross-bridge and edge. Cups with small but prominent knobs on surface; margin with fine finger-like projections. Cups circular in outline, with a cross on one face and a square on the other, with a large central hole and four oblong marginal perforations. Occasionally cups with smooth margins (Fig. 7B) occur. Tail ossicles essentially the same as ossicles elsewhere. Anal

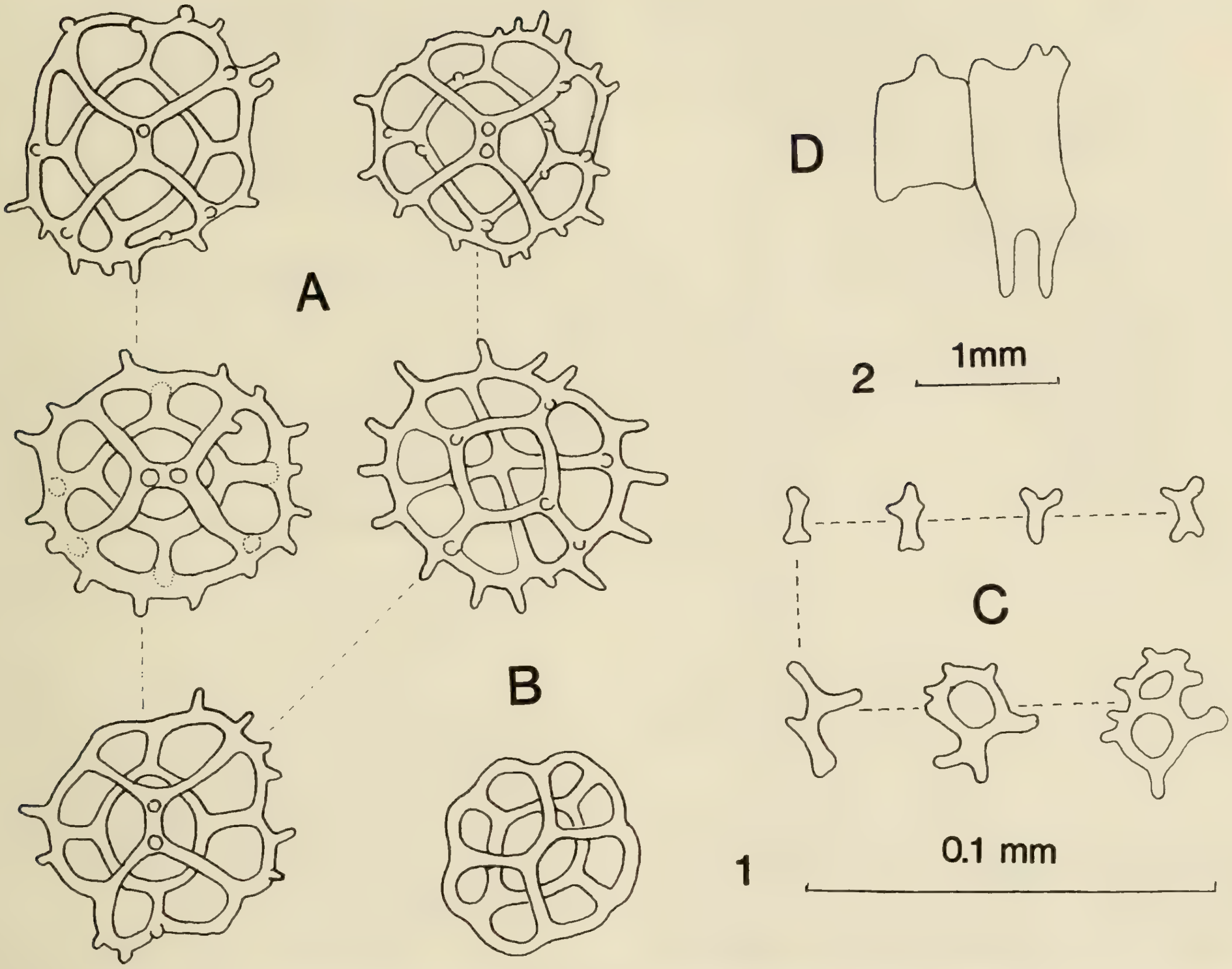

Fig. 7. *Paracaudina delicata,* new species. A, crossed cups from body wall; B, crossed cups with smooth edge; C, ossicles from anal projections; D, radial and interradial pieces of calcareous ring.

projections present, in form of minute irregular rods and plates (Fig. 7C).

Remarks.—*Paracaudina delicata* is unique in having delicate crossed cups with fine projections around the margin. Small individuals of *Paracaudina chilensis* have crossed cups of similar basic structure (Hozawa 1928, Pawson 1963), but they differ in several details (see Figs. 7A, 8).

Distribution.—Known only from a single specimen from the Gulf of Tonkin, at a depth of 21 m.

Paracaudina chilensis (Müller)
Fig. 8

Molpadia chilensis Müller, 1850:139.

Caudina ransonnetii von Marenzeller, 1881: 126.

Caudina chilensis.—Hozawa, 1928:361, pls. 14–17.—Chang, 1934:29, pl. 3, fig. 3, textfig. 15.—Yang, 1937:22, pl. 4, fig. 3, textfig 13.

Pseudocaudina ransonnetii.—Heding, 1931: 283.

Paracaudina ransonnetii.—Heding, 1932: 455.

Paracaudina chilensis var. *ransonnetii.*—H. L. Clark, 1935:281; 1938:540; 1946: 444.—Chang & Liao, 1964:45.

Paracaudina chilensis.—Pawson, 1963:10; 1970:49, pl. 2, fig. 2.—A. M. Clark & Rowe, 1971:184, fig. 96A.

Material examined.—Numerous specimens from the Yellow Sea, Xiemen (Amoy), Fujian Province and Zhanjiang, Guangdong Province.

Remarks.—This is one of the most common molpadiid holothurians in China. It is

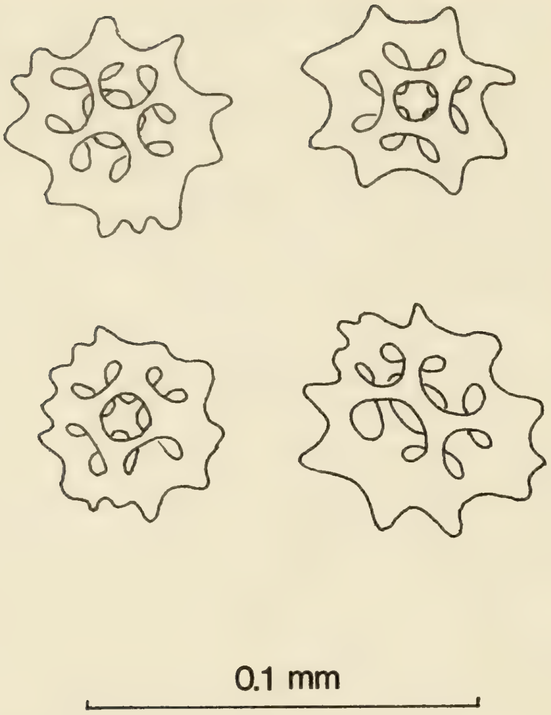

Fig. 8. *Paracaudina chilensis,* (Müller). Crossed cups from body wall of 30 mm specimen.

particularly abundant in the Yellow Sea, but in Southern China it seems to be uncommon, being known only from Xiemen (Amoy), Fujian Province and Zhanjiang, Guangdong Province. The animals live buried in sandy mud near lowtide mark, with the body directed downwards, and the posterior end at the surface of the substrate, for purposes of respiration. Color in life is white, often with a slight purplish tinge. Ossicles of a small specimen of 30 mm total length are illustrated here (Fig. 8) for comparison with those of *P. delicata,* n. sp.

Distribution.—Widespread in the circum-Pacific, known from Australia, Japan, California, Florida, Chile and New Zealand, in depths of 9–990 m (Pawson 1970). In China, it is known to range from Dalian, Liaodong Peninsula to Zhanjiang, Leizhou Peninsula, in littoral and sublittoral depths.

Genus *Acaudina* H. L. Clark, 1907

See Heding, 1931:284; H. L. Clark, 1946: 445.

Diagnosis.—Tentacles with only one pair of lateral digits. Tail practically absent, inconspicuous. Ossicles smooth or spinose thick plates, often doughnut-shaped with one or more perforations. Ossicles usually absent from body wall, but often found close to posterior end of body.

Key to species of *Acaudina* known from China

1. Ossicles more or less scarce, sometimes wanting, sometimes present only at posterior of body; in form of small oval bodies with one or sometimes a few holes; also more or less irregular perforated plates or dumbbell-shaped bodies or spinose thick plates may occur .... *molpadioides* (Semper, 1868)
– Ossicles more or less numerous, in form of small oval plates with three or four holes, a few doughnut-shaped bodies, and short, irregularly branched particles with broad blunt branches .... *leucoprocta* (H. L. Clark, 1938)

Acaudina molpadioides (Semper)

Haplodactyla molpadioides Semper, 1868: 41, pls. 9, 10, figs. 2a, 4, 5, 9; pl. 13, fig. 3.
Acaudina molpadioides.—H. L. Clark, 1946: 445.—Chang & Liao, 1964:46.—A. M. Clark & Rowe, 1971:184, fig. 96b, pl. 31, fig. 12.—A. M. Clark, 1982:489, 495.—Liao, 1984:250, textfig. 1.

Material examined.—695 specimens, collected at many localities ranging from the Gulf of Tonkin and Hainan Island northward to Qingdao, Shandong Province.

Remarks.—This is one of the most common and most variable holothurians in China, but it has not yet been reported from the Xisha Islands and Liaoning Province. After studying the rich material, we agree with Sluiter (1912) that *A. molpadioides* is a single highly variable species. We regard *A. delicata* (H. L. Clark) as a synonym of *A.*

molpadioides; the plates of *A. delicata* with serrated edges on perforations are found only in young animals, and they disappear as the animals grow.

Distribution.—Widely distributed in the Indo-Malayan region in 0–330 m.

Acaudina leucoprocta (H. L. Clark)

Aphelodactyla leucoprocta H. L. Clark, 1938: 543, fig. 60.

Acaudina leucoprocta.—H. L. Clark, 1946: 446.—A. M. Clark & Rowe, 1971:184.—Liao, 1984:252, textfigs. 2–3.

Aphelodactyla irania Heding, 1940:124, fig. 7.

Acaudina irania.—A. M. Clark & Rowe, 1971:184.

Material examined.—112 specimens from the Gulf of Tonkin to the East China Sea.

Remarks.—The occurrence of this big caudinid holothurian in large numbers on the southern coast of China is of great interest. It was originally described from three specimens collected near Broome, Northwestern Australia. The present material ranges from 20 to 270 mm in length. The smaller specimens conform to the description of *A. irania* (Heding) in all characteristics; we believe that *A. irania* as characterized by Heding merely represents young stages of *A. leucoprocta*.

In the body wall of smaller individuals the ossicles are almost all small, plump ring- or doughnut-shaped bodies, while in full-grown specimens they become small oval plates with 3 or 4 holes. In the Chinese specimens the ossicles seem to be more numerous than in Australian specimens. The color is typically dark purple or purplish brown, with the area around the anus light gray.

This is one of the most common large holothurians in China, and it is particularly abundant in the vicinity of Zhoushan Archipelago, Zhejiang Province, where it is used for beche-de-mer, and it is marketed at Shanghai as "sweet fish."

Distribution.—Western Australia, Iran and China (ranging from the Gulf of Tonkin to the East China Sea), in depths of 15–122 m.

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STATUS OF TYPE SPECIMENS OF *PLATYCEPHALUS RODERICENSIS* CUVIER, 1829 AND *P. BORBONIENSIS* CUVIER, 1829 (PISCES: PLATYCEPHALIDAE)

Leslie W. Knapp

Abstract.—The type specimens of *Platycephalus rodericensis* Cuvier do not agree well with the original description and the name has been applied to several different species. Further, as the types for both *P. rodericensis* and *P. borboniensis* Cuvier represent species that have not been reported in the western Indian Ocean beyond the coast of India or the Persian Gulf, it is unlikely that they came from Reunion Island as stated by Cuvier. Despite the confusion, *P. rodericensis* is here interpreted as the senior synonym of *P. timoriensis* Cuvier, *P. sculptus* Günther, and *Insidiator detrusus* Jordan & Seale. *P. borboniensis* Cuvier is regarded as a junior synonym of *Inegocia japonica* (Tilesius, 1812).

In 1829, Cuvier & Valenciennes published volume 4 of "Histoire Naturelle des Poissons." Included was a treatment of the Platycephalidae with descriptions of numerous new species. Although most of these species descriptions have been correctly interpreted in the literature, several have caused nomenclatural problems that persist to date. The purpose here is to point out the improper usage of these names in recent publications and to provide clarification of their status.

Based on specimens said to have been collected by Mylius at Île Bourbon (Reunion), Cuvier *in* Cuvier & Valenciennes (1829:253) described *Platycephalus rodericensis* from syntypes said to be three and one-half pouces in total length (ca. 95 mm). The description also stated that *P. rodericensis* has 12 soft dorsal-fin rays, 12 anal-fin rays, a large, strong preopercular spine, four strong spines on the suborbital ridge, and brown spots on the fins. Sauvage (1873) redescribed *P. rodericensis,* duplicating Cuvier's description more or less verbatim but adding several additional measurements. He described the spots on the fins as being black rather than brown and selected the larger syntype, "with a length of 105 mm," as being "the type of the species." This qualifies as a lectotype designation. The lectotype retains the original catalog number Muséum National d'Histoire Naturelle (MNHN) 6838 and the paralectotype has been recataloged as MNHN 1992-0002. The total lengths of the two specimens were recorded as 89 and 192 mm by Blanc & Hureau (1968). The putative types differ from Cuvier's description in several respects. They have 11 (not 12) dorsal-fin rays. Further, the species represented by the putative types of *P. rodericensis* does not have brown spots on the fins and has been found no closer to Reunion Island than the Gulf of Oman and the coast of India. The possibility exists that the original types of *P. rodericensis* were lost and replaced with other specimens. Several searches by me through the general flathead collection at MNHN failed to unearth any specimens that could possibly have been the types.

Despite the apparent discrepancies, I feel that Cuvier's description of *P. rodericensis* was probably based on the putative types. The body length measurement (ca. 95 mm) given by Cuvier is reasonably close to the total lengths of the MNHN types. In looking at Cuvier's descriptions of other new flatheads, he frequently differed in fin-ray counts from the counts that I have taken from his type specimens so a difference of one dorsal-fin ray is not unexpected. Explaining away the lack of dark spots in the fins is more difficult. The spinous dorsal fin of the species represented by the types of *P. rodericensis* can have two rather large blotches but the other fins are unspotted, being primarily dusky.

Part of Cuvier's description of *P. rodericensis* (large preopercular spine, four strong spines on the suborbital ridge, lateral line scales with small spines on anterior part of the body) fits either the types or another species currently referred to as *Suggrundus macracanthus* Bleeker, 1869. Like *P. rodericensis, S. macracanthus* is known from the northern Indian Ocean, but has not been reported from as far south as Reunion Island. The latter species has 12 soft dorsal-fin rays, well-developed dark spots in the fins and has been identified as *P. rodericensis* by Troschel (1840) and de Beaufort (1962), *Repotrudis rodericensis* by Kuronuma & Abe (1986), and *Suggrundus rodericensis* by Shao & Chen (1987).

I regard as significant Cuvier's statement that the interorbital space of *P. rodericensis* is narrow, going three times or less into the vertical eye diameter. This agrees with the condition that I found in the MNHN types. The same measurement in *S. macracanthus* goes twice or less in the vertical eye diameter and is a good character for separating the two species. Although the evidence is not entirely supportive, I believe that Cuvier did describe *P. rodericensis* from the putative types, with the mention of spots in the fins apparently being erroneous.

In addition to the features of the syntypes of *P. rodericensis* given above, the presence of a finger-like subopercular flap, pored lateral-line scales each with a single pore opening to the exterior, and the configuration of spines and ridges on the head indicate the types of *P. rodericensis* to be the same species as the type specimen of *P. timoriensis*, a species described by Cuvier on the page following his description of *P. rodericensis*. Cuvier did indeed note some similarities between the two nominal species. A brief synonymy follows.

Suggrundus rodericensis
(Cuvier, 1829)

Platycephalus rodericensis Cuvier *in* Cuvier & Valenciennes 1829:253 (original description, type locality, Ile Bourbon).—Sauvage, 1873:58 (Ile Bourbon).

Platycephalus timoriensis Cuvier *in* Cuvier & Valenciennes 1829:254–255 (original description, type locality, Timor).

Platycephalus sculptus Günther, 1880:41–42, pl. XVII, fig. A (original description, type locality, Arafura Sea).—de Beaufort, 1962:148–149 (Arafura Sea).

Insidiator detrusus Jordan & Seale, 1905: 15, pl. X (original description, type locality, Hong Kong).

Insidiator macracanthus.—McCulloch, 1914:141–142 (in part) (Bowen, Queensland).

Thysanophrys sculptus.—Kamohara, 1952: 106 (Urado and Mimase, Shikoku Prefecture).—Wongratana, 1975:5, pl. I, fig. 3 (Thailand).

Kumococius detrusus.—Matsubara & Ochiai, 1955:92–94, pl. II (Urado, Shikoku Prefecture).—Masuda et al., 1984: 322, pl. 289–A,B (Tosa Bay to South China Sea).—Kuronuma & Abe, 1986:80 (Arabian Gulf, Hong Kong and Japan).

Platycephalus bengalensis Rao, 1966:123–127, fig. 1 (original description, type locality, Bay of Bengal).—Talwar & Kacker, 1984:336, fig. 137 (northeast coast of India).

Suggrundus rodericensis.—Knapp, 1983: no pagination (Gulf of Oman to Japan and Australia) (misspelled *rodricensis*).—Gloerfelt-Tarp & Kailola, 1984: 123, fig. on 122 (North West Shelf of Arafura Sea).—Sainsbury et al., 1985:118, fig. on 119 (North West Shelf to Arafura Sea).—

Shao & Chen, 1987:82, figs. 13–14 (Indo-Pacific, Philippines, Taiwan to Queensland).—Paxton et al., 1989:471 (off Western Australia and Northern Territory).

Another species described by Cuvier in 1829, *Platycephalus borboniensis,* was also alleged to have been collected at Reunion Island by Mylius. Cuvier's description stated that the holotype was 162 mm in total length (I measure 166 mm), had 13 soft dorsal-fin rays (I count 12) and 12 anal-fin rays, two spines on the suborbital ridge under the eye, two short preopercular spines, and a rather narrow interorbital space. The specimen agrees quite well with the original description and the name appears to be a junior synonym of *Inegocia japonica* (Tilesius, 1812). As the range of *I. japonica* is known from Madras and Sri Lanka to Japan and Australia, Cuvier's Reunion Island record for *P. borboniensis* seems to be in error.

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HYLA BOCOURTI (MOCQUARD, 1899), A VALID SPECIES OF FROG (ANURA: HYLIDAE) FROM GUATEMALA

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Abstract.—The taxonomic history of *Hyla bocourti* is reviewed. *Hyla bocourti* is a valid species inhabiting the northeastern highlands of Guatemala. Adult males of this species differ from all other members of the *Hyla eximia* group in having large dorsal tubercles that are capped with black, pointed, keratinous spines.

The taxonomic status of the small hylid frog from the northern highlands of Guatemala described by Mocquard (1899) as *Hyliola bocourti* has been a matter of some confusion. This population of hylids previously had been referred to *Hyla regilla* Baird & Girard (1852) by Brocchi (1877, 1881), who stated that Bocourt had found them in abundance in the highlands of "Vera Paz" [=Alta Verapaz] near Cobán, Guatemala. On the basis of Mocquard's description and a specimen from the type series provided by the Paris Museum, Günther (1901) also recognized *H. bocourti.* Taylor (1939) synonymyzed *H. bocourti* with *H. euphorbiacea* Günther (1859), and expressed the opinion that Brocchi's (1881) *Hyla regilla* was not the same as Mocquard's (1899) *Hyliola bocourti* because of differences in dorsal and posterior thigh coloration. Taylor's (1939) actions were apparently based solely on descriptions in the literature and he makes no mention of having examined any material from Guatemala.

Stuart (1948) revived the name *H. bocourti,* noting that "The re-establishment of [*H. bocourti*] as a valid species is as tentative as was Taylor's procedure." He pointed out that the description of the series of frogs and the figures by Brocchi (1881) were not in complete agreement and that an independent description of a specimen from this series (Günther 1901) varied in some respects from information provided by Brocchi. Further obfuscating this issue, Brocchi (1881) included specimens from California, Tehuantepec, and Alta Verapaz. Stuart (1963) continued to recognize *H. bocourti* in his checklist of the herpetofauna of Guatemala.

Duellman (1970) placed the name *H. bocourti* back into the synonymy of *H. euphorbiacea,* stating that, on the basis of the limited material available to him, the two taxa could not be distinguished from each other. Duellman & Campbell *in* Frost (1985), under the comments for *H. euphorbiacea,* suggested that *H. bocourti* might be a distinct species, but provided no evidence.

We examined *H. euphorbiacea* from Oaxaca, Mexico, *H. walkeri* from Chiapas, Mexico, and *H. bocourti* from Guatemala, and find that these species differ in a number of morphological characters (see Definition and Diagnosis). On the basis of morphology and biogeography, *H. bocourti* may be more closely related to *H. walkeri* of Guatemala and Chiapas than it is to *H. euphorbiacea,* but nevertheless it is a distinct species (see Table 1).

We herein present a redescription and diagnosis for *H. bocourti* and comment on what is known of its natural history. For ease of comparison, we have followed the format of Duellman (1970).

Table 1.—Comparison of measurements (mm), proportions, and other morphological characteristics of adult *Hyla bocourti*, *H. euphorbiacea*, and *H. walkeri*. Character abbreviations SVL, snout–vent length; TL, tibia length; FL, foot length; HL, head length; HW, head width. Means in parentheses.

Character	*Hyla bocourti* (♂♂ = 79; ♀♀ = 15)	*Hyla euphorbiacea* (♂♂ = 44; ♀♀ = 6)	*Hyla walkeri* (♂♂ = 48; ♀♀ = 9)
Snout–vent length [SVL]			
Males	26.3–34.6 (30.2)	30.6–38.6 (34.9)	30.2–38.1 (34.2)
Females	29.2–37.7 (33.7)	35.3–43.4 (38.1)	33.7–38.5 (35.9)
TL/SVL			
Males	0.46–0.55 (0.50)	0.45–0.52 (0.49)	0.48–0.55 (0.51)
Females	0.48–0.55 (0.50)	0.49–0.52 (0.51)	0.49–0.57 (0.53)
FL/SVL			
Males	0.43–0.54 (0.46)	0.43–0.50 (0.47)	0.44–0.52 (0.48)
Females	0.42–0.50 (0.46)	0.43–0.52 (0.49)	0.47–0.52 (0.49)
HW/SVL			
Males	0.30–0.38 (0.35)	0.33–0.37 (0.35)	0.32–0.38 (0.35)
Females	0.32–0.37 (0.34)	0.33–0.35 (0.34)	0.31–0.36 (0.33)
HL/SVL			
Males	0.24–0.35 (0.31)	0.28–0.33 (0.30)	0.23–0.30 (0.26)
Females	0.27–0.33 (0.31)	0.27–0.31 (0.30)	0.23–0.28 (0.26)
Tympanum diameter/Eye size			
Males	0.39–0.79 (0.56)	0.43–0.72 (0.57)	0.39–0.75 (0.56)
Females	0.41–0.75 (0.58)	0.47–0.61 (0.56)	0.50–0.63 (0.58)
Snout in dorsal profile	Acuminate	Acutely rounded	Acutely rounded
Nuptial excrescences (♂♂)	Black spines	Pale spinules	Pale spinules
Hand webbing formula	II 2–3 III 3–2½ IV	II 2–3 III 3–3 IV	II 2½–3½ III 3½–2½ IV
Toe disc size	Larger than finger discs	Smaller than finger discs	Smaller than finger discs
Foot webbing formula	I 1–2 II 1–2 III 1½–2 IV 2–1½ V	1 2–2 II 1½–3 III 2–3 IV 3–2 V	I 2–2½ II 2–3 III 2¼–3 IV 3¼–2 V
Skin on dorsum (♂♂)	Tuberculate	Smooth	Smooth
Dorsal coloration	Usually tan	Usually green	Green
Coloration posterior surface of thigh	Large yellow spots	Small yellow spots	Uniformly tan

Redescription of Hyla bocourti.—Males of this species attain a maximum snout–vent length of 34.6 mm, and females reach 37.7 mm. In a series of 79 adult males from the departamentos de Alta and Baja Verapaz, Guatemala, the snout–vent length is 26.3–34.6 ($\bar{X}$ = 30.2) mm; the ratio of tibia length to snout–vent length is 0.46–0.55 ($\bar{X}$ = 0.50); the ratio of foot length to snout–vent length is 0.43–0.54 ($\bar{X}$ = 0.46); the ratio of head length to snout–vent length is 0.24–0.35 ($\bar{X}$ = 0.31); the ratio of head width to snout–vent length is 0.30–0.38 ($\bar{X}$ = 0.35), and the ratio of the diameter of the tympanum to the size of the eye is 0.39–0.79 ($\bar{X}$ = 0.56). Fifteen adult females from the same region have snout–vent lengths of 29.1–37.7 ($\bar{X}$ = 33.7) mm, and do not differ significantly in proportions, including relative tympanum size.

The head is narrower than the body, and the top of the head is flat. In dorsal profile the snout is acuminate, and in lateral profile is slopes dorsally from about the level of the nares, ventrally it is truncate. The snout is moderately long, and the slightly protuberant nostrils are situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is angular, and the loreal region is barely concave; the lips are thick and barely flared. A dermal fold extends posteriorly from the eye, above the tympanum, and diffuses onto the body above the insertion of the arm. The fold covers the upper edge of the tympanic annulus, and the remainder of the tympanic ring is obscure to moderately well developed. The tympanum is separated from the eye by a distance about one-half of the diameter of the tympanum.

The arms are moderately long and slender; a poorly developed axillary membrane extends about one-fourth to one-third the length of the upper arm. A weak transverse dermal fold is present on the wrist. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are small, indistinct, and present only on the proximal segments of the digits. A small, round palmar tubercle is present. The prepollex is enlarged, and in breeding males bears a nuptial excrescence consisting of many dark spines. These black nuptial spines are usually present on the medial edges of fingers II and III and on the ventral surfaces of the distal portion (exclusive of discs) of fingers II–IV. The webbing on the hand is vestigial, with a webbing formula (Myers & Duellman 1982) of II 2–2⅔ III 2½–2½ IV. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A transverse dermal fold is not evident on the heel; a distinct tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, ovoid, and barely elevated. The outer metatarsal tubercle, if present, is small and subconical. The toes are long and slender and bear discs that are larger than those on the fingers. The subarticular tubercles are moderately small and round, and the supernumerary tubercles are low, indistinct, and present only on the proximal segments of the digits. The toes are about three-fourths webbed, with a webbing formula of I 1½–2 II 1–2 III 1–2 IV 2–1½ V.

The cloacal opening is directed posteroventrally at mid-level of the thighs, and a short cloacal sheath is evident. In adult males, the skin on the dorsum, including that of the hind limbs, is tubercular often with dark, keratinous spines (Fig. 1). These spines usually are present on the sides of the head in the loreal and tympanic regions, including on the tympanum and the upper eyelid, and on the elbows, cloacal area, and lateral surfaces of the foot. Females lack these tubercles and have relatively smooth skin on the dorsal surfaces. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular in both sexes. The tongue is cordiform, slightly notched behind, and free posteriorly for about one-fifth of its length. The dentigerous processes of the vomers are small posteromedially inclined elevations between the posterior margins of the small, round choanae. Five males have two to four ($\bar{X} = 2.9$) vomerine teeth and five females have four to seven ($\bar{X} = 4.8$) vomerine teeth on each process. The vocal sac is bilobate and subgular.

The general coloration of *Hyla bocourti* is dorsum tan, yellowish brown, or yellowish green; males tend to be tan and females tend to be greenish. Most specimens have irregular brown blotches on the dorsum and three or four dark bars on both the fore- and hind limbs. A dark brown stripe extends from the snout through the nostril, eye, and

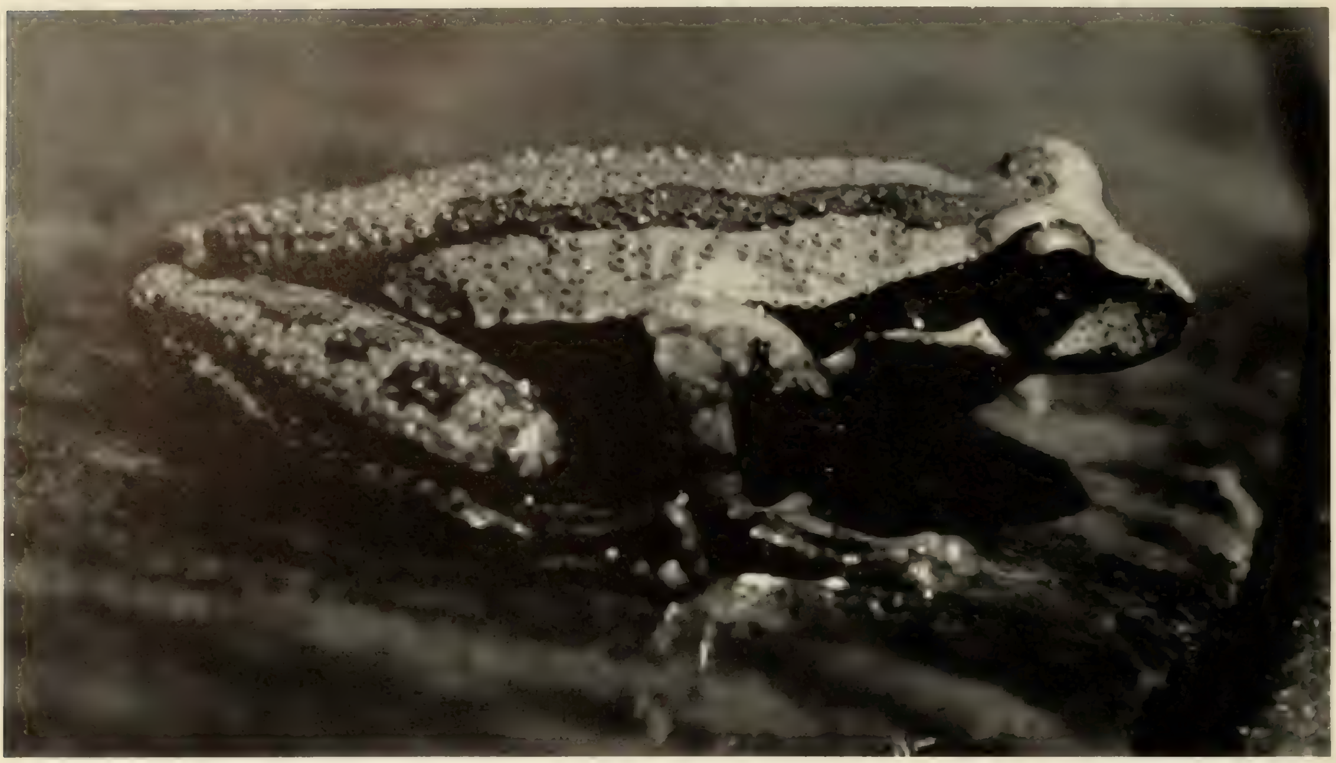

Fig. 1. Adult male *Hyla bocourti* from near Purulhá, Departamento de Baja Verapaz, Guatemala. Dark keratinous spines are clearly evident on the dorsum.

tympanum onto the flanks; this stripe is bordered above by a narrow pale line. The groin is heavily mottled with yellow and the posterior surfaces of the thighs are reticulated with dark brown and spotted with yellow. The belly is creamy white. The iris is yellow.

Definition and diagnosis.—A frog of the *Hyla eximia* group (Duellman 1970) in which adult males have a strongly tuberculate skin with black keratinous spines and enlarged prepollex with a nuptial excrescence of relatively large black spines. The toes are about three-fourths webbed, with a webbing formula of I 1½–2 II 1–2 III 1–2 IV 2–1½ V; the toe discs are larger than finger discs.

Hyla bocourti differs from *H. walkeri* and *H. euphorbiacea* in having a snout that is acuminate rather than acutely rounded in dorsal view, in having the toe discs that are larger rather than smaller than the finger discs, and in having toes that are about three-fourths rather than about one-half webbed. Adult male *H. bocourti* have tuberculate dosral skin, often with black keratinous spines, and prepollices with black spines, whereas in *H. euphorbiacea* and *H. walkeri* the dorsal skin is smooth and the nuptial excrescences are white to tan with minuscule spinules.

The dorsal coloration of *H. bocourti* is tan, yellowish brown, or yellowish green, not the verdant green of *H. walkeri* and usually of *H. euphorbiacea.* The posterior surface of the thigh in *H. bocourti* has relatively large yellow spots in comparison with *H. euphorbiacea* which has small yellow spots; in *H. walkeri* the posterior surface of the thigh is uniformly tan. The upper lip is margined with a distinct white stripe in *H. euphorbiacea* and *H. walkeri*; this stripe is absent in *H. bocourti.* The subgular sac is bilobate in male *H. bocourti,* median in *H. euphorbiacea* and *H. walkeri.*

An ANOVA performed on the residuals of the regression of head width and head length revealed significant differences ($P < 0.001$) among species; *H. bocourti* has a relatively narrower head (Fig. 2). Significant differences ($P < 0.001$) also existed among

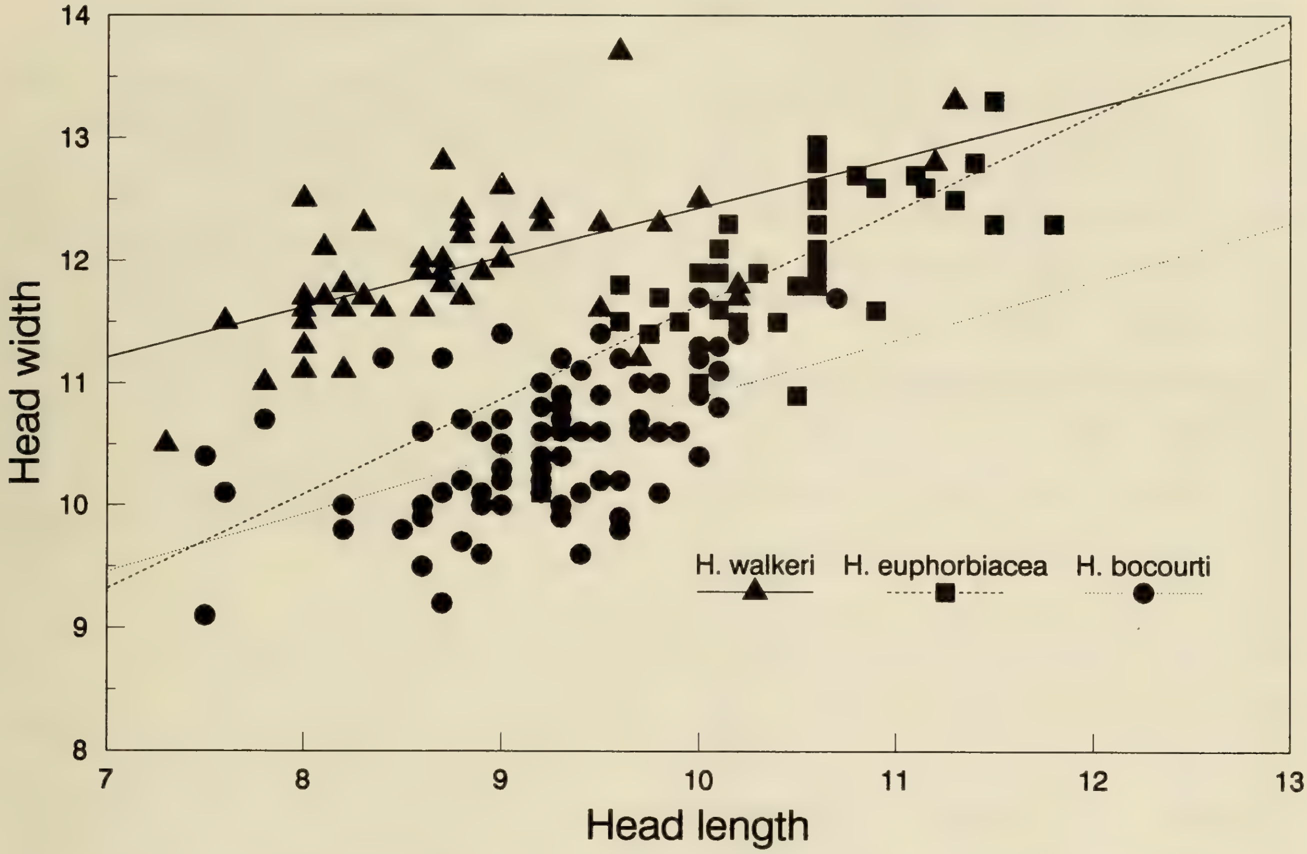

Fig. 2. Relationship between head width and head length in males of the southern members of the *Hyla eximia* group.

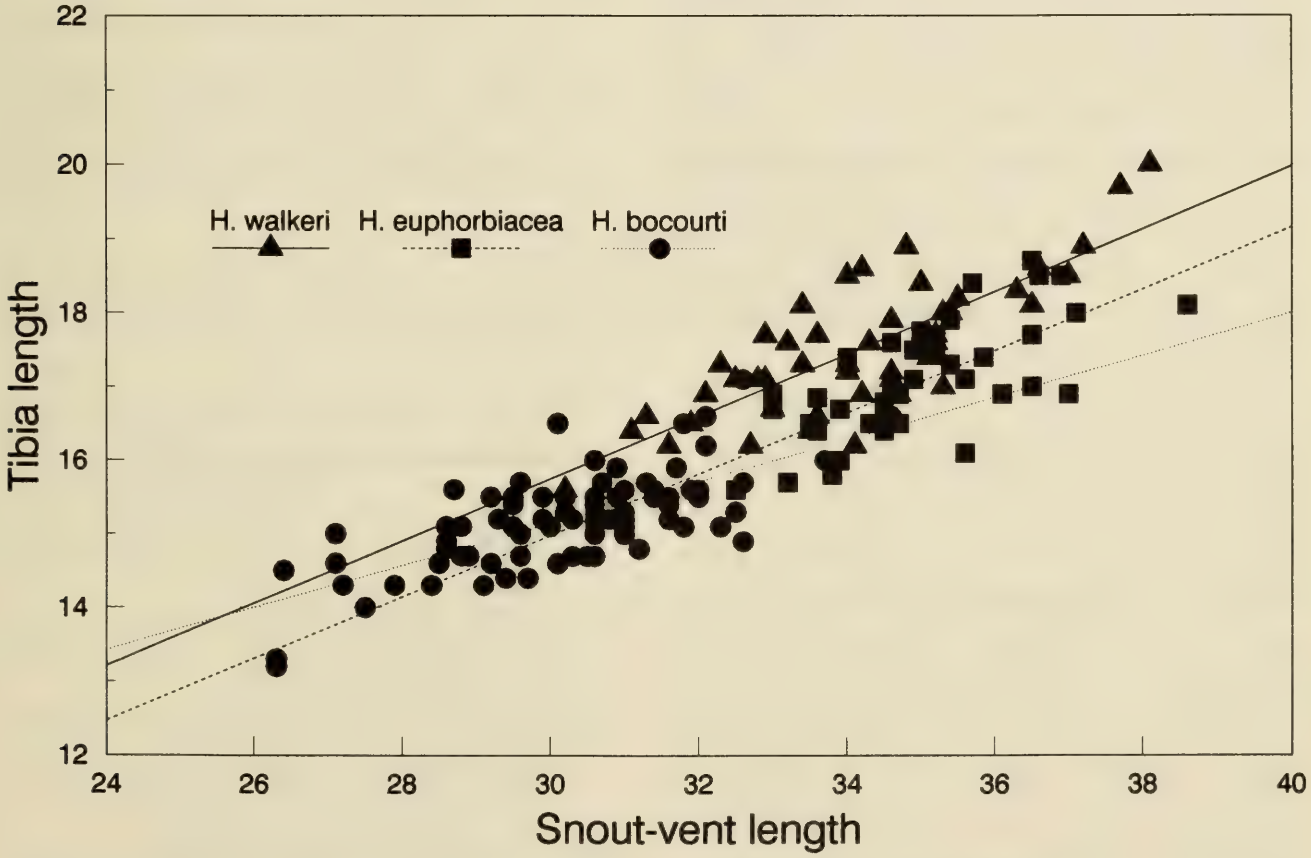

Fig. 3. Relationship between tibia length and snout–vent length in males of the southern members of the *Hyla eximia* group.

species for the relative length of the tibia (Fig. 3).

Natural history notes.—Hyla bocourti is known with certainty only from the highlands of Alta and Baja Verapaz, Guatemala. Stuart (1963) recorded this species from the Sierra de los Cuchumatanes, but records from this mountain range are most probably referable to *H. walkeri.*

Our field experience suggests *H. bocourti* is mostly terrestrial. Our specimens (UTA) all have been taken from open grassy meadows, devoid of trees. We have found these frogs in great abundance during the early part of the rainy season (June) when these meadows are flooded. Other specimens were reported from beneath leaf sheaths of bananas and from a bromeliad (Stuart 1948). The tadpoles of this species are unknown.

Specimens examined.—Hyla bocourti. Guatemala: *Alta Verapaz:* Cafetal just W Rta. Nac. 5, 10.4 mi (by road) S Cobán, 1470 m (MVZ 109370–77); 11 km NW Tactic (KU 129857–58); *Baja Verapaz:* Cerro Quisís (UTA A-5505); 2.4 mi NW (by road) Purulhá (UTA A-7693–769); 0.0–2.4 mi SE Purulhá on CA-14 (UTA A-7770); 4.2 km W western Purulhá turnoff (UTA A-17255–58); 4.5 km W western Purulhá turnoff (UTA A-17259–61); 4.8 km W Purulhá, 1524 km (KU 186362); 3.8 km W Purulhá, 1536 m (KU 186363–75); 3.2–5.3 km W Purulhá 1530 m (KU 186376–421); Purulhá (KU 186422).

Hyla euphorbiacea. Mexico: *Oxaca:* 2.4 mi SE Tlacolula turnoff (UTA A-696); Sierra Juárez, Llano de las Flores, 2786 m (UTA A-13235–63, 17134–53).

Hyla walkeri. Mexico: *Chiapas:* ca. 6 mi NW San Cristóbal de Las Casas (UTA A-4345); 6.8 mi ESE San Cristóbal de Las Casas (UTA A-7435); 3.2 km E Teopisca (UTA A-13397); 6.4 km SE San Cristóbal de Las Casas, Grutas de San Cristóbal, 2286 m (UTA A-13398–432); 7.7 km SE San Cristóbal de Las Casas, 2304 m (UTA A-13433–52); 9.0 km NW Pueblo Nuevo Solistahuacán, 1829 m (UTA A-13453).

Acknowledgments

We thank William E. Duellman and John E. Simmons for the loan of specimens and color slides of *H. bocourti* (taken by JAC) housed in the University of Kansas (KU) collection; these slides, in conjunction with JAC field notes, provide the basis for the color description of the species. We are also grateful to Harry W. Greene for the loan of specimens from the Museum of Vertebrate Zoology (MVZ), to Darrel R. Frost for providing us with bibliographic material, and to Daniel R. Formanowicz for his statistical advice.

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DESIGNATION OF A LECTOTYPE FOR *CROCODYLUS RANINUS* S. MÜLLER AND SCHLEGEL (REPTILIA: CROCODYLIDAE), THE BORNEO CROCODILE

Charles A. Ross

Abstract.—The type series of *Crocodylus raninus* is a composite of three species: *Crocodylus siamensis* from Java, *Crocodylus porosus* and *Crocodylus raninus* (sensu Ross 1990) from Borneo. Designation of a lectotype (RMNH 3219) restricts the type locality of *C. raninus* to Pontianak, Kalimantan Barat, Indonesian Borneo, and reaffirms its validity as a distinct Bornean species.

In resurrecting *Crocodylus raninus* S. Müller & Schlegel, 1844 (Ross 1990), I made two assumptions: that the type series contained only two Bornean specimens and that only two species of *Crocodylus* occur on Borneo. A more complete translation of Müller & Schlegel's (1844) article, examination of crocodilian specimens in the Nationaal Natuurhistorisch Museum, Leiden [formerly Rijksmuseum van Natuurlijke Historie (RMNH)], and circumstantial evidence received from biologists working in Borneo, prove the first assumption incorrect, and make the second suspect. These new data do not negate the validity of *C. raninus* but do necessitate the designation of a lectotype for this species.

Müller & Schlegel (1844:15–18) discussed variation in *Crocodilus biporcatus* Cuvier, 1807 (=*Crocodylus porosus* Schneider, 1801) and differentiated five specimens then in the RMNH collection from it. They used the name *raninus* (1844:26) to designate the new taxon which they had referred to as a blunt-snouted race (1844:15–18), distinct from typical *C. porosus.* They also figured two specimens without number or other identifying marks, an adult skull and a juvenile, as *C. raninus* (1844, pl. 3, figs. 7 and 8).

These five specimens were extant and, in the absence of a formal designation of type material, must be considered syntypes. Additional material in the collection of "Luitenant-Kolonel Henrici" of Borneo was mentioned by Müller & Schegel (1844:16) but was not available to them in Leiden and was not included in their description. Another RMNH specimen collected by Kuhl and van Hasselt in Java was originally identified as *Crocodylus rhombifer* Cuvier, 1807, by Boie, and reidentified by Müller & Schlegel (1844:15) as *C. vulgaris* Cuvier, 1807 (=*Crocodylus niloticus* Laurenti, 1768) and now identified as *Crocodylus siamensis* Schneider, 1801, by RMNH staff, also has no bearing on the type series of *C. raninus.*

Museum abbreviations follow Leviton et al. (1985).

The syntypes include two juvenile crocodiles collected by Boie and Macklot at Tjikao (=Kao Tji, Jawa Barat), Java, in 1827. One of these (RMNH 21695) was originally prepared as a mounted specimen but subsequently had its stuffing removed and now is stored as a dry skin with its skull and mandibles separate. The other (SMF 8090, received on exchange from RMNH) was prepared as a whole alcoholic specimen but now has its skull and mandibles removed and separate. These specimens are *C. siamensis* Schneider, 1801; both skulls have the longitudinal interorbital ridge characteristic of *C. siamensis* and their skins have granular anterior throat scales unlike any other extant crocodile species (see Ross 1990).

Another juvenile syntype (a whole alcoholic specimen, RMNH 3219) was collected by P. Diard at Pontianak (Kalimantan Barat), Borneo, and referred to (correctly) by me (1990) as *C. raninus.*

The other syntypes are adult skulls listed by Lidth de Jeude (1898) as "n" and "p" and remain so marked in the RMNH collection. Six measurements for both skulls, contrasted with similarly sized skulls of *C. porosus,* were given by Müller & Schlegel (1844:17) making identification of these syntypes certain. The largest skull (n), collected in the interior of Borneo by Müller in 1836, is a *C. porosus*; it is large (64.5 cm from the posterior margin of the cranial table to tip of snout), has the lachrymal ridges well developed and nearly parallel and distinct to the ninth maxillary tooth, and a palatine-pterygoid suture directed strongly posteriorly and partially dissecting the pterygoid (see Ross 1990).

The other skull (p), collected from a tributary of the Banjer River (tributary of Sungai Barito, Kalimantan Tengah), Borneo, by Müller in 1836, is smaller (45.0 cm, measured as above) and although slightly deformed is *C. raninus* sensu Ross (1990); its palatine-pterygoid suture is nearly transverse, there is no longitudinal interorbital ridge, and the lachrymal ridges are poorly developed.

The identification of RMNH 3219 as a species of crocodile from Borneo distinct from *C. porosus* and *C. siamensis* on the basis of dermal characteristics (25 transverse ventral scale rows, four postoccipital scales, and 38–39 transverse throat scale rows) is clear and it is herein designated as lectotype for *C. raninus* S. Müller & Schlegel. The four other specimens (paralectotypes) form a composite series of *C. porosus* (RMNH n) and *C. raninus* (RMNH p) from Borneo and *C. siamensis* (RMNH 21695 and SMF 8090) from Java.

Discussion

Live *C. siamensis* (identified by throat squamation and other external characters) have recently been discovered at commercial crocodile farms in Kalimantan, Borneo (G. Webb, in litt.). There is no certainty that these animals originated from Borneo and none have, so far, been found in the wild. *Crocodylus siamensis* historically does occur on Java (MZB 3, Ancol, Jawa Barat; MZB 15, Donau, Banten (Serang District), Jawa Barat; RMNH 21695 and SMF 8090, Kao Tji, Jawa Barat) and is present in crocodile farms in Jakarta (Ross, pers. obs.). Its natural occurrence on Borneo, while doubtful, can not be casually dismissed although historic references to palustrine crocodiles in Borneo refer to *C. raninus.*

The distribution and status (both population and taxonomic) of Indonesian crocodiles remain poorly known. Examination of most available museum specimens suggests that palustrine crocodiles were widespread in the Indonesian islands and problematic material from Amboin (ZMA uncat., IRSNB 3919), Sumatra (RMNH uncat.), Bangka (RMNH 21687–9), Simaloer (RMNH uncat.) and Sulawesi (USNM 42834), have been examined but require further study pending accumulation of additional specimens.

Acknowledgments

I thank Marinus S. Hoogmoed (RMNH), Konrad Klemmer (SMF), Mathias Lang (IRSNB), Bertus van Tuijl (ZMA), and P. Boeadi (MZB), for allowing examination of critical material in their respective collections. I am especially appreciative of Henry Heuveling v Beek (Universiteit van Amsterdam) who tirelessly translated the entire Müller & Schlegel (1844) article for me and Franklin D. Ross (MCZ) who examined IRSNB specimens at my request. Travel necessary to examine specimens at MZB and in the environs of Jakarta was partially supported by a Smithsonian Institution Research Opportunities Fund Grant. The hospitality and assistance of Chuck L. Darsono and his family (Shanti, Richard, and Anastasia) of Cengkareng, Jakarta, made my first brief visit to Indonesia not only productive, but extremely pleasant. Research space and encouragement was provided by W. R. Heyer and G. R. Zug, Division of Amphibians and Reptiles, USNM. R. I. Crombie, T. F. Fritts, and G. R. Zug reviewed a draft of this paper.

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MORPHOLOGICAL DIFFERENTIATION BETWEEN *RHOGEESSA MINUTILLA* AND *R. TUMIDA* (MAMMALIA: CHIROPTERA: VESPERTILIONIDAE)

Luis A. Ruedas and John W. Bickham

Abstract.—Two nominal species of *Rhogeessa, R. minutilla* and *R. tumida,* co-occur in tropical South America. The distinction between these two species is based on somewhat ambiguous morphological characters (LaVal 1973). To better distinguish the two species, univariate and multivariate analyses were performed on 19 cranial and osteological characters. Ten were found to differ significantly between the two species based on univariate analyses. All but two of these were significant in the multivariate analyses. Thus, the two species are morphologically well differentiated. A key based on the morphometric analyses is presented to facilitate the identification of the two *Rhogeessa* species.

The genus *Rhogeessa,* exclusively Neotropical in distribution, contains five or six species (Goodwin 1958, LaVal 1973, Ramirez Pulido 1982, Nowak & Paradiso 1983), of which two, *R. minutilla* and *R. tumida,* occur in South America. *Rhogeessa minutilla* was described by Miller (1897; Type: USNM 63216, male) from Margarita Island, off the coast of Venezuela. The species ranges as far north on the mainland as Panama and is broadly distributed throughout mainland Venezuela and Colombia. *Rhogeessa tumida,* described from Veracruz, Mexico, by Allen (1866; Type: USMN 84012, male), overlaps the distribution of *R. minutilla* from Panama to Venezuela. Because the two species are so difficult to distinguish morphologically (LaVal 1973), Smith & Genoways (1974) suggested that *R. minutilla* probably is a geographic race of *R. tumida.* The purpose of this report is to evaluate the morphological differentiation of these taxa and the validity of *R. minutilla* as a distinct species.

Methods

Characters examined.—Ten individuals of each species were measured for 19 cranial and wing-bone characters (Fig. 1). Cranial characters (abbreviations in parentheses) included: Breadth of braincase (BB); Condylobasal length (CBL); depth of braincase (DB); greatest length of skull (GLS); mastoid breadth (MB); length of mandibular toothrow (MTL); length of maxillary toothrow (MXT); postorbital breadth (POB); postpalatal length (PPL); width across upper canines (WUC); and width across upper molars (WUM). Wing-bone measurements (taken from dried skins) are length of forearm (FA); metacarpal of digit 3 (IIIm); first (proximal) phalanx of digit 3 (IIIp1); second phalanx of digit 3 (IIIp2); metacarpal and first phalanx of digit 4 (IVm and IVp); and metacarpal and first phalanx of digit 5 (Vm and Vp). Zygomatic breadth, a character commonly employed in morphometric analyses, was not used because most of the specimens examined had damaged zygomatic arches.

Measurements were taken to the nearest 0.01 mm with digital calipers. Statistical analyses were performed on AT&T 6386 WGS or Compaq Deskpro 386/33 microcomputers using the Statistical Analysis System software, version 6.03 (SAS Institute Inc., 1988a, 1989b). Tests of normality were performed invoking the normal option

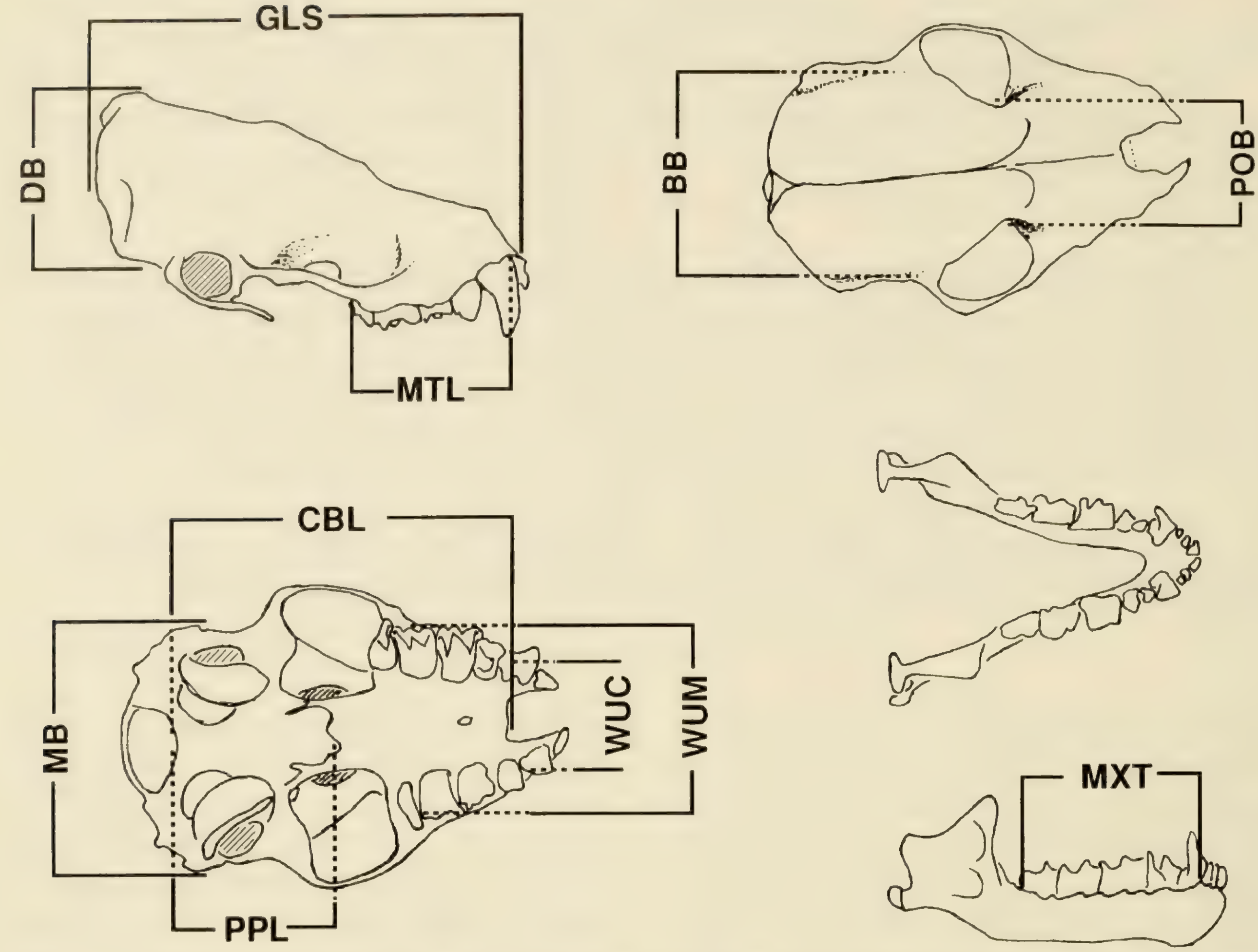

Fig. 1. Cranial measurements taken for the morphological analysis of *Rhogeessa minutilla* and *R. tumida* carried out herein. Abbreviations are explained in the methods section. Skull drawing based on Texas Cooperative Wildlife Collection specimen 9488, *R. tumida*, female, Veracruz, Mexico.

of the UNIVARIATE procedure, which tests for normality using the Shapiro-Wilk statistic, W, and provides the associated probability value. Sexual dimorphism in each character was evaluated using a *t*-test (PROC TTEST). Sexes were grouped for characters where no sexual dimorphism was found, and a *t*-test carried out to determine which characters were significantly different between species, given that the intent of the exercise was to distinguish between the two nominal taxa. Characters found to differ significantly between the two species then were used in multivariate analyses grouping the taxa both a priori (canonical discriminant analysis, PROC CANDISC) and a posteriori (principal component analysis, PROC PRINCOMP). A discriminant function analysis (PROC DISCRIM) was used to develop discriminant criteria to classify each individual. Classification error rates were obtained using posterior probability estimates based on crossvalidation, said to reduce both the bias and variance of the estimator (Hora & Wilcox 1982).

Materials Examined

Rhogeessa minutilla.—Venezuela: Lara; Caserio Boro, 10 km N El Tocuyo, 9°53′N, 69°47′W, 6 males (USNM 455998, 456000, 456002, 456005–456007), 4 females (USNM 456003, 456004, 456009, 456028).

Rhogeessa tumida.—Venezuela: Trujillo, 25 km NW Valera, near Agua Santa, 9°32′N, 70°40′W, 1 female (USNM 372488); Falcon, 19 km NW Urama, km 40, 10°37′N, 68°24′W, 1 female (USNM 374018), Apure,

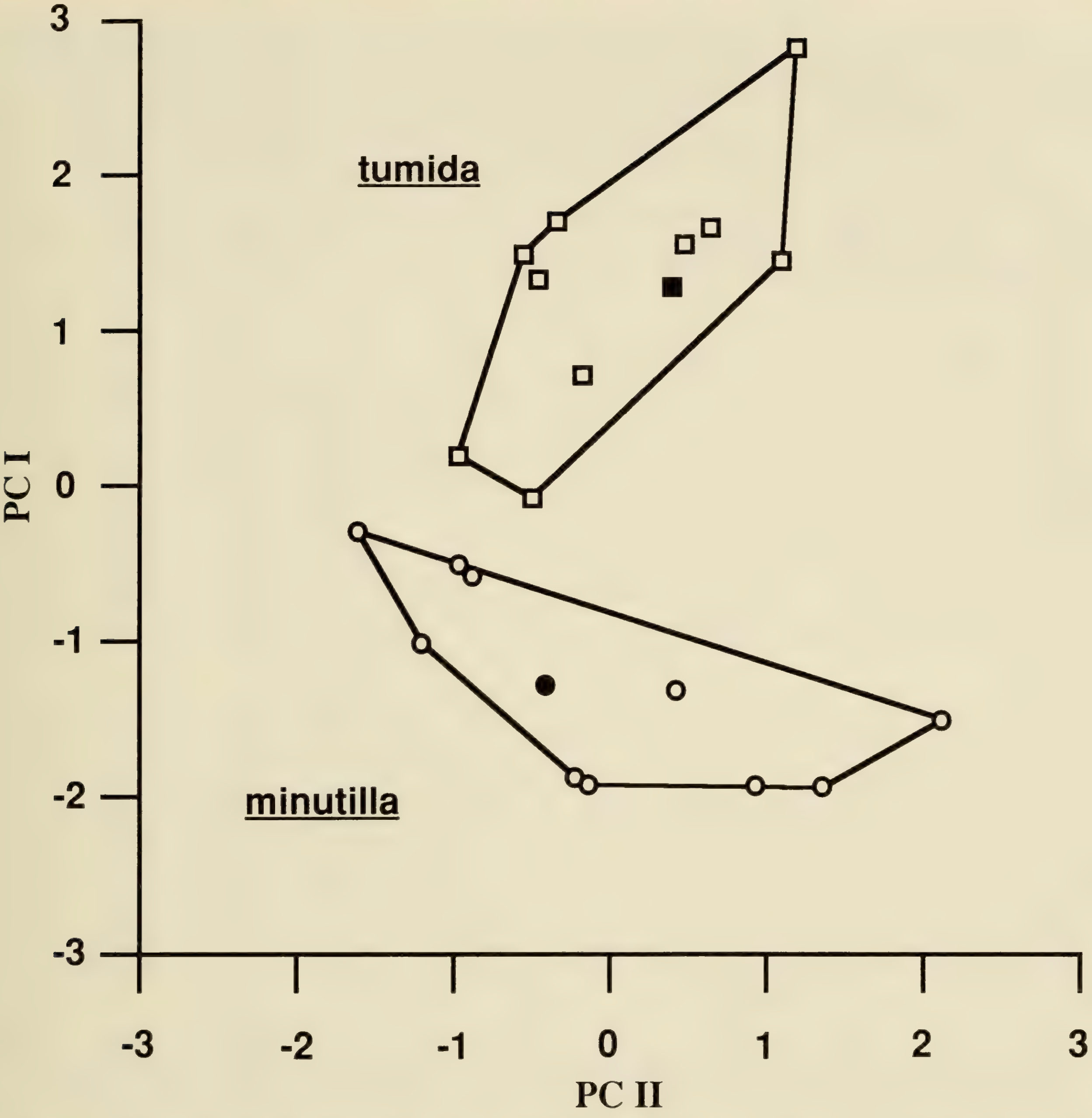

Fig. 2. Plots of the first and second principal component scores (PC I and PC II, respectively) from the principal component analysis carried out with *R. minutilla* and *R. tumida* based only on forearm length, breadth of braincase, mandibular toothrow, and length of first phalanx of digit four. Group centroids are represented by darkened shapes.

Hato Cariben; La Villa, 32 km N Puerto Paez, 6°33′N, 67°13′W, 1 female (USNM 374019); Miranda, 7 km E Rio Chico, near Puerto Tuy, 10°20′N, 65°54′W, 1 female (USNM 387737); Miranda, 1 km E Rio Chico, 10°19′N, 65°58′W, 1 male (USNM 387738); Sucre, 26 km ESE Carupano (Manacal), 10°37′N, 63°01′W, 1 female (USNM 409487); Yaracuy, 20 km NW San Felipe (Minas de Aroa), 10°25′N, 68°54′W, 1 male (USNM 441774), 1 female (USNM 441775); Miranda, 13 km SE Caracas, near El Encantado, 10°27′N, 66°47′W, 1 female (USNM 441776); Aragua, 3 km S Ocumare de la Costa, 10°24′N, 67°46′W, 1 male (USNM 517507).

Results

Of the 19 mensural characters examined (Table 1) sexual dimorphism was encountered only in two, in contrast with species

Table 1.—Measurements (mm) of the 19 characters used in the analysis to differentiate between *R. minutilla* and *R. tumida*. Number refers to specimen number (United States National Museum, see specimens examined). Abbreviations of characters are: BB, breadth of braincase; CBL, condylobasal length; DB, depth of braincase; FA, forearm measurement (dry); GLS, greatest length of skull; MB, mastoid breadth; MTL, length of mandibular toothrow; MXT, length of maxillary toothrow; POB, postorbital breadth; PPL, postpalatal length; WUC; width across upper canines; WUM, width across upper molars. Abbreviations of digital measurements are: IIIm,

Number $P > \|t\|$	Sex	BB 0.0030	CBL 0.0195	DB ns	GLS ns	MB 0.0132	MTL[1]	MXT 0.0059	POB 0.0340	PPL ns
R. minutilla										
455998	M	5.7	9.3	4.7	12.9	6.7	5.9	4.7	3.0	4.4
456000	M	5.6	9.4	4.4	11.9	6.2	5.4	na	3.3	4.2
456002	M	5.6	8.9	4.3	11.8	6.3	5.5	4.4	3.2	4.2
456005	M	5.6	9.0	4.4	11.8	6.6	5.3	4.3	3.0	4.3
456006	M	5.6	8.7	4.4	12.1	6.5	5.4	4.4	3.0	4.1
456007	M	5.5	9.1	4.8	12.2	6.6	5.7	4.7	3.1	4.3
456003	F	5.4	9.8	4.4	12.3	6.3	6.0	4.7	2.9	4.4
456004	F	5.6	9.5	4.3	12.0	6.5	5.8	4.5	3.1	4.1
456009	F	5.6	9.0	4.6	12.0	6.6	5.6	4.5	3.0	4.4
Means		5.62	9.20	4.53	12.16	6.50		4.56	3.05	4.30
SE		0.036	0.107	0.066	0.116	0.056		0.057	0.041	0.044
R. tumida										
387738	M	5.8	9.1	4.6	12.0	6.8	5.4	4.4	3.1	4.2
441774	M	6.0	8.8	4.0	11.9	6.6	5.4	4.4	3.4	4.4
517507	M	5.6	8.8	4.7	11.8	6.7	5.4	4.2	3.3	4.1
372488	F	6.0	8.5	4.0	11.7	6.5	5.4	4.0	3.0	4.2
374018	F	5.8	9.0	4.1	12.1	6.6	5.4	4.4	3.0	4.4
374019	F	5.0	9.0	4.5	12.0	6.8	5.6	4.2	3.2	4.3
387737	F	5.9	8.9	4.4	12.4	6.9	5.6	4.4	3.3	4.0
409487	F	5.5	9.0	4.3	12.0	5.5	5.5	4.4	3.3	4.0
441775	F	6.1	9.1	4.5	12.6	6.8	5.7	na	3.1	4.3
441776	F	6.1	8.9	4.4	12.1	7.1	5.5	4.5	3.3	4.0
Means		5.87	8.90	4.35	12.08	6.72		4.34	3.20	4.19
SE		0.063	0.053	0.072	0.084	0.055		0.043	0.048	0.046

[1] Length of mandibular toothrow was sexually dimorphic in both putative species. Means (*SE*) were: *R. minutilla*, males 5.53 (0.086), females, 5.88 (0.121), $P > |t| = 0.0403$; *R. tumida*, males 5.40 (0.010), females 5.52 (0.045), $P > |t| = 0.0417$. Interspecific comparisons of this character within sexes showed no significant differences between males, but highly significant differences between females, $P > |t| = 0.0077$.

[2] Length of second phalanx of digit three was sexually dimorphic in *R. tumida*: males 10.05 (0.321), females 10.46 (0.210), $P > |t| = 0.0417$.

of *Rhogeessa* found in Central America, where females average 4% greater in linear measurements (Hall 1981). Length of mandibular toothrow (LMT) was significantly different between sexes in both *R. minutilla* ($P > |t| = 0.0403$) and *R. tumida* ($P > |t| = 0.0417$). The proximal phalanx of digit three was sexually dimorphic in *R. tumida* only ($P > |t| = 0.0417$). These characters therefore were not used in subsequent multivariate analyses, although it should be noted that LMT was significantly different between females of either species ($P > |t| = 0.0077$). An additional seven characters were not significantly different between the species, and were omitted from subsequent analyses; these were DB, GLS, PPL, WUM, IIIm, IIIp2, and Vm.

The remaining characters were included in the first round of multivariate analyses. The model including all variables that were significant in the *t*-test was itself significant

Table 1.—Continued.

metacarpal of digit 3; IIIpl, first (proximal) phalanx of digit 3; IIIp2, second phalanx of digit 3; IVm, IVp1, and Vm, Vp1, metacarpal and proximal phalanx of digits four and five, respectively. All finger bone measurements are from dried skins. The *P* values reported below cranial character abbreviations are the results of the interspecific *t*-test comparisons; ns indicates no significant differences between the species.

WUC 0.0450	WUM ns	FA 0.0004	IIIm ns	IIIp1[2]	IIIp2 ns	IVm 0.0287	IVp 0.0001	VM ns	Vp 0.0143
3.7	5.4	27.6	28.0	11.7	10.2	27.6	9.8	27.9	7.6
3.5	na	27.0	26.2	10.8	8.8	25.6	8.8	27.0	7.0
3.5	5.0	26.7	26.2	10.4	10.0	25.4	8.7	26.7	6.8
3.3	5.0	26.9	27.3	11.0	8.2	25.8	8.6	26.7	6.5
3.5	5.2	26.8	26.6	11.1	10.0	25.7	9.1	26.0	7.1
3.6	5.3	26.7	27.0	11.4	9.2	25.9	9.3	26.7	7.3
3.6	5.5	27.3	26.8	11.4	9.0	26.3	9.0	26.3	6.8
3.5	5.3	27.3	25.7	10.2	8.7	25.1	9.2	26.8	6.8
3.6	5.4	26.6	27.4	10.7	10.0	26.3	9.6	26.4	7.2
3.57	5.28	26.98	26.85	10.99	9.39	26.06	9.15	26.74	7.04
0.041	0.054	0.104	0.217	0.149	0.216	0.233	0.123	0.158	0.106
3.4	5.0	28.7	28.4	10.4	10.0	27.4	8.8	27.8	7.1
3.6	5.4	27.6	26.2	9.9	9.3	25.9	8.3	26.4	6.7
3.4	5.0	28.0	27.7	9.8	9.7	27.6	8.6	27.3	6.6
3.4	5.2	27.1	26.8	10.1	8.9	26.5	8.1	26.8	6.2
3.4	5.4	29.1	27.0	10.4	9.3	26.2	8.3	26.3	6.2
3.4	na	29.3	28.1	10.6	10.0	27.9	8.4	26.9	7.0
3.4	5.2	29.2	27.8	10.5	9.2	26.8	8.4	27.6	6.9
3.5	5.1	28.4	27.0	10.8	9.5	26.0	8.7	26.4	6.6
na	5.1	28.2	26.9	10.4	8.8	26.7	8.2	27.2	6.7
3.6	5.4	30.6	27.5	10.4	8.9	27.2	8.4	27.1	6.4
3.46	5.19	28.62	27.34	10.33		26.82	8.41	26.98	6.64
0.027	0.058	0.308	0.212	0.095		0.218	0.070	0.166	0.100

($P > F = 0.0449$), but it was found that width across upper canines and length of first phalanx of digit five were not significant in the multivariate model. A second round of multivariate tests was carried out using only BB, CBL, MB, MXT, POB, FA, IVm and IVp. The multivariate model in this case was highly significant ($P > F = 0.0077$). Using these eight measurements, the two South American species distinctly segregate into groups composed of individuals of either species using both a priori (canonical discriminant analysis, CANDISC) and a posteriori (principal component analysis, PRINCOMP) multivariate tests (Table 2, Fig. 2).

Notwithstanding the clear separation of the two species in multivariate space, three individuals were misclassified in the discriminant analysis: one *R. minutilla* (USNM 456002) was classified as *R. tumida* and two *R. tumida* (USNM 372488 and 441774) were classified as *R. minutilla.*

Discussion

Morphological approaches to questions of species identity are compounded in *Rhogeessa* where the presence of chromosomally distinct populations indicates several potentially cryptic species (Bickham & Baker 1977, Baker 1984, Baker & Bickham

Table 2.—First and second raw canonical coefficients (Can1 and Can2) from the canonical discriminant analysis, and first and second eigenvectors (Prin1 and Prin2) from the principal component analysis carried out on the 10 individuals of each species of *Rhogeessa* discussed in the text. The first canonical vector accounted for all the interspecific variation in the canonical discriminant analysis. In the principal component analysis, all variation was accounted for by the first four principal components (52.1%, 26.5%, 14.0%, and 7.4%, respectively); the first component principally accounts for interspecific differences. The results of the principal component analysis are graphically summarized in Fig. 2.

Character	Can1	Can2	Prin1	Prin2
FA	1.0463	−0.2826	−0.5300	0.2503
PIV	−1.9812	−0.6352	−0.4335	0.5962
BBCS	1.3335	3.0157	0.3884	0.7447
MTR	−1.2991	3.3186	0.6167	0.1651

1986, Baker et al. 1985). In this study, we found ten characters that differed significantly at $\alpha = 0.05$. Thus, from a morphometric standpoint, there appears to be little evidence to support the contention of Smith & Genoways (1974) that *R. minutilla* probably will result in being no more than a geographic race of *R. tumida.* However, populations of *Rhogeessa* are extremely interesting and complex from an evolutionary perspective. Although it is improbable that morphology alone will clarify the phylogenetic relationships among *Rhogeessa* species (LaVal 1973), morphological studies combined with chromosomal and biochemical work may prove useful (Bickham & Baker 1977, Baker et al. 1985). Indeed, as currently known (LaVal 1973, Bickham & Baker 1977, Honeycutt et al. 1980), the South American populations identified herein as the species *R. tumida* represent at least two species. Specimens from Venezuela and Trinidad have karyotypes with a diploid number (2N) of 30, whereas a specimen from Suriname had 2N = 52 (Honeycutt et al. 1980, Baker et al. 1985). Clearly, additional studies of this species, and of *R. minutilla,* are needed and should include chromosomal and biochemical analyses as well as morphological assessment to help clarify relationships within this taxon.

Although there is great overlap in the mensural characters examined, a key to South American species of *Rhogeessa* was constructed based on the above morphometric analyses; additional characters not included in the key may be used as necessary:

1. Color paler; forearm usually shorter than 27.60 mm; first phalanx of digit IV usually longer than 8.62 mm .... *Rhogeessa minutilla*

– Color darker; forearm usually longer than 27.13 mm; first phalanx of digit IV usually shorter than 8.84 mm .... *Rhogeessa tumida*

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2780	*Platyscelis* Latreille, 1818 (Insecta, Coleoptera): proposed designation of *Tenebrio hypolithus* Pallas, 1781 as the type species, so conserving *Oodescelis* Motschulsky, 1845.
2773	*Schizopus* Le Conte, 1858 (Insecta, Coleoptera): proposed conservation.
2749	*Eristalis* Latreille, 1804, *Helophilus* Fabricius, 1805, *Xylota* Meigen, 1822 and *Eumerus* Meigen, 1822 (Insecta, Diptera): proposed conservation.
2730	*Cheilosia* Meigen, 1822 and *Pyrophaena* Schiner, 1860 (Insecta, Diptera): proposed conservation.
2552	*Anniella pulchra* Gray, 1852 (Reptilia, Squamata): proposed designation of a neotype.
2746	*Anas arcuata* Horsfield, 1824 (currently *Dendrocygna arcuata*; Aves, Anseriformes): proposed conservation of the specific name.

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CONTENTS

The lumbrinerids (Annelida: Polychaeta) collected in two northwestern Atlantic surveys with descriptions of a new genus and two new species Ann B. Frame 185

A new species of *Dentatisyllis* (Syllidae: Polychaeta) from Cape Verde Islands, West Africa Eduardo López García and Guillermo San Martín Peral 219

A new arabellid polychaete living in the mantle cavity of deep-sea wood boring bivalves (family Pholadidae) Harlan K. Dean 224

Thaumatoconcha pix, a new bathyal and abyssal species from off SE Australia (Ostracoda: Halocyprida: Thaumatocyprididae) Louis S. Kornicker 233

A new species of *Anthessius* (Copepoda: Poecilostomatoida) associated with *Berthella stellata* (Risso, 1826) (Gastropoda: Opisthobranchia) P. J. López-González, M. Conradi, S. Naranjo, and J. C. García-Gómez 240

Cyclopoid and harpacticoid copepods (Crustacea) from southeastern Alaska, U.S.A. Teruo Ishida 249

Tortanus (*Acutanus*) *angularis*, new subgenus and new species (Copepoda: Calanoida), from the Caribbean Sea, with remarks on the subgenera in the genus *Tortanus* Susumu Ohtsuka 255

Euryte verecunda, new species (Copepoda: Cyclopoida), associated with the coral *Porites lobata* on the Pacific coast of Panama Arthur G. Humes 268

Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Farran, 1913) (Oithonidae) from a mangrove cay in Belize Frank D. Ferrari and Julie W. Ambler 275

Renocila loriae and *R. richardsonae* (Crustacea: Isopoda: Cymothoidae), external parasites of coral reef fishes from New Guinea and the Philippines Ernest H. Williams, Jr. and Lucy Bunkley-Williams 299

Guitonia troglophila, a new genus and species of anchialine crab from the Galápagos, Isla Santa Cruz, Grieta de Caleta la Torta (Crustacea: Decapoda: Brachyura) John S. Garth and Thomas M. Iliffe 310

Description of a new *Axianassa* (Crustacea: Decapoda: Thalassinidea) from Brazil, and its first larval stage Sérgio de A. Rodrigues and Roberto Munehisa Shimizu 317

Two new callianassid shrimps from Brazil (Crustacea: Decapoda: Thalassinidea) Sérgio de A. Rodrigues and Raymond B. Manning 324

Mesocyclops guangxiensis, new species, and new records of four congeners (Crustacea: Copepoda: Cyclopidae) from China, Laos, and Viet Nam Janet W. Reid and Brian H. Kay 331

A collection of Thalassinidea (Crustacea: Decapoda) from the Pacific coast of Colombia, with description of a new species and a checklist of eastern Pacific species Rafael Lemaitre and Gabriel E. Ramos 343

Procambarus (*Ortmannicus*) *attiguus*, a new troglobitic crayfish (Decapoda: Cambaridae) from the Saint Johns River basin, Florida Horton H. Hobbs, Jr. and Richard Franz 359

A new genus of Periscelididae (Diptera) from the Neotropics Wayne N. Mathis and László Papp 366

Molpadiid sea cucumbers of China, with descriptions of five new species (Echinodermata: Holothuroidea) David L. Pawson and Yulin Liao 373

Status of type specimens of *Platycephalus rodericensis* Cuvier, 1829 and *P. borboniensis* Cuvier, 1829 (Pisces: Platycephalidae) Leslie W. Knapp 389

Hyla bocourti (Mocquard, 1899), a valid species of frog (Anura: Hylidae) from Guatemala Jonathan A. Campbell and Dwight P. Lawson 393

Designation of a lectotype for *Crocodylus raninus* S. Müller and Schlegel (Reptilia: Crocodylidae), the Borneo crocodile Charles A. Ross 400

Morphological differentiation between *Rhogeessa minutilla* and *R. tumida* (Mammalia: Chiroptera: Vespertilionidae) Luis A. Ruedas and John W. Bickham 403

International Commission on Zoological Nomenclature: Applications 410

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A PLEA FOR ADEQUATE CITATION OF AUTHORS OF TAXA IN SYSTEMATIC STUDIES

Douglas A. Kelt and R. Eduardo Palma

Abstract.—We note a lack of standardization of citations to authors of animal taxa in scientific journals, probably due to the absence of such requirements by the International Code of Zoological Nomenclature (ICZN 1985). We feel that this omission is regretful and that such citation requires greater attention by reviewers and editors. This is underscored by the fact that those areas where access to older literature is most difficult (e.g., South America, southeast Asia) are also areas where further systematic investigations are most pressing and where the number of energetic and well educated systematists is increasing. Here we present a standardized citation format, based on ICZN recommendations, which provides clear and complete citation to the original description of a taxon, and we recommend that this format be accepted as standard for citation of authors of animals in scientific literature.

In the zoological systematic literature there is a notable absence of standard and complete citations to authors of taxa. Indeed, in many journals there appears to be no standard policy for such references. Recent changes and modifications proposed for the International Code of Zoological Nomenclature (ICZN 1985, Savage 1990) do not address this problem. We would like to comment on two points which we feel merit greater concern, and to propose a standardized format for citation of authors of scientific names in the literature. We address this comment principally to works of taxonomic and systematic focus, although we recognize its relevance to certain non-systematic works as well.

Background

The zoological and botanical codes differ in their views on citation of taxon names. Article 46 of the Botanical Code states clearly: "For the indication of the name of a taxon to be accurate and complete . . . it is necessary to cite the name of the author(s) who validly published the name concerned" (ICBN 1988). In contrast, the Zoological Code considers the citation of authors (including the date of publication) to be optional (ICZN 1985, Article 51a), although it is recommended both in the text (ICZN 1985, Appendix E:10) and the literature citation (ICZN 1985, Appendix E:14). Neither code mandates citation of the date of the original description.

Ideally, the first reference to a taxon in a publication should include the author of that name, and the year in which the name was published (CBE 1983; ICZN 1985, Article 51b). Unfortunately, many journals either do not require authorship citation, or have no policy for standardized citations.

A distinction should be made here between (a) journals that do not include citations to taxon descriptions in the Literature Cited, and which, therefore, may not allow author citations in the text, and (b) journals that allow citation in the text, but not in the Literature Cited. The former is consistent but incomplete, whereas the latter example is inconsistent and should be amended. In a survey of 25 widely circulated journals in systematics, we found only 14 to have made efforts to include both text and Literature Cited references to authors of taxonomic names.

Perhaps the most important concern, however, is the common failure to cite nomenclatural authorships in the Literature Cited section. Of the 25 journals surveyed, only eight have a policy requiring such citation and here again, most were inconsistent.

Recommendations

Text citation.—In an attempt to remedy this situation we suggest the following format for text citations of authors of taxonomic names. The first reference to a taxon should include the author(s) and the year in which it was originally described. This would take one of the following forms: *Aus bus* Smith & Jones, 1991; and *Cus bus* (Johnson & Brown, 1992). The first example is the one used and recommended by the Zoological Code (ICZN 1985, Article 51). It clearly states the name of the taxon and authors of that taxon, and the year the taxon was described. Use of parentheses in the second example is proper when the species was originally described in a different genus but later subsumed under *Cus* (see ICZN 1985, Article 51c). The ICZN recommends the use of commas between the authors and the date (Recommendation 22a), and we support following that style. Any subsequent references to the taxon would obviously not require inclusion of the author or date.

More complex situations are considered in recommendations to Article 51 of the Zoological Code (ICZN 1985). While these are considered optional by the ICZN, we recommend that journals follow the recommendations of the ICZN as follows. If the name of a taxon was proposed anonymously, but its authorship is known or may be inferred, the name of the author should be enclosed in square brackets to indicate the original anonymity (e.g., *Aus bus* [Smith & Jones, 1991]; Recommendation 51a). If the original description was made by an author other than the author of the publication containing the description, or of some subset of the joint authors, such authorship may be made clear as *Aus bus* Smith & Jones, 1991 in Johnston, 1991, or *Cus bus* (Johnson & Brown, 1992 in Smith, Johnson, & Brown, 1992) (Recommendation 51b). Finally, if it is desired to cite both the original author of a species-group as well as the person who transferred it to a new genus, the following format should be observed: *Cus bus* (Smith & Jones, 1991) Johnson & Brown, 1992 (Recommendation 51c).

Literature citation.—The obvious solution to the problem of inadequate or missing citations to literature referenced in the text is to require such citation in the Literature Cited section. A reference to Allen (1903), for example, does the reader little benefit without a reference to the journal and pagination of the article.

Appropriate citation of references given in synonymies is often unclear. We feel that these should be listed in the Literature Cited as are other text citations (literature in botanical synonymies may be considered different because of the availability of the Botanico-Periodicum-Huntianum (Lawrence et al. 1968) and Taxonomic Literature (Stafleu & Cowan 1976)).

Discussion

The absence of authorship citation makes it difficult and time-consuming to locate original descriptions for older taxa. This concern is not trivial, as laborious library searches may be required to find papers which could otherwise be readily obtained. This problem is magnified tremendously for investigators in developing countries, who frequently lack sophisticated communication systems and the quality of library services found among libraries in developed countries. It is relevant to note here that these are precisely regions of the world where further systematic investigations are in greatest need, and where the number of well educated and energetic scientists is rapidly increasing. Although there are some references where many of these citations may be found (e.g., Hooker & Jackson 1895, and supplements for the botanical literature; Honacki et al. 1982, for mammals; Frost 1985, for amphibians; King & Burke 1989, for crocodilians, tuatara, and turtles), it remains the responsibility of the author to provide the citations for those taxa that are reported. Moreover, published checklists rarely provide synonymies, leaving the reader unable to trace names of taxa not currently used.

We write this comment in the hope that it will stimulate editors and reviewers to require more consistent referencing to taxonomic descriptions, especially in systematic and taxonomic papers. We suggest that a uniform set of citation standards be embraced by the scientific community, and that journals publishing scientific names conform to these standards. The formats outlined here provide such a standard. Far from academic, this practice begs greater attention. Standardized complete citations for taxon names and their authors should facilitate nearly all investigations in systematic biology.

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A NEW SUBSPECIES OF *CHAMAEA FASCIATA* (WRENTIT) FROM OREGON (AVES: TIMALIINAE)

M. Ralph Browning

Abstract.—Geographic variation in plumage color of *Chamaea fasciata* (Wrentit) from northern California and southern Oregon is related to climate. A new subspecies, *Chamaea fasciata margra,* is described from a disjunct population of southern interior Oregon. Colonization of *C. fasciata* in interior Oregon was perhaps from birds crossing coniferous forests via isolated balds of *Ceonothus.* Recent increases of Wrentits in interior Oregon may be in response to habitat alterations (deforestation, fires) and concurrent global warming.

Chamaea fasciata (Wrentit) is a permanent resident from northwestern Oregon to northern Baja California. The American Ornithologists' Union (A.O.U. 1957) and Deignan (1964) recognized six subspecies: *C. f. phaea* Osgood, from the humid coastal belt of northwestern Oregon to the California border; *rufula* Ridgway, from the humid coastal belt of northern California to Marin Co.; *intermedia* Grinnell, from the interior and southern areas of the San Francisco Bay region; nominate *fasciata* Gambel, from coastal Monterey Co. to central San Luis Obispo Co., California; *henshawi* Ridgway, from central interior and southern coastal California to the border of Mexico, with a disjunct population in interior southwestern Oregon; and *canicauda* Grinnell & Swarth, from Baja California. Phillips (1986) recognized only four subspecies, treating *intermedia* as a synonym of nominate *fasciata* and *canicauda* as a synonym of *henshawi.* He characterized *phaea* as the darkest subspecies, *rufula* as darker than nominate *fasciata,* and *henshawi* as the palest and grayest subspecies.

Phillips (1986:179) stated that birds from northcentral California are "highly variable" and that "*fasciata*-like" birds range north to Oregon. Although Phillips did not mention specimens from southern interior Oregon west of the Cascades, he referred to two specimens from Klamath Falls, Klamath Co., east of the Cascade Mountains, as "too rich below for *henshawi.*" He also reported that Swarth had identified the two specimens as "intermediate between *phaea* and *henshawi* . . . simulating *fasciata,*" but Phillips (1986) stated that "surely *phaea* is not involved." Although birds from the interior of northern California and southern Oregon were discussed by Phillips in his "Remarks" section under *henshawi,* he did not identify them to subspecies, and gave the northern range of this pale subspecies as central California. I compared specimens of *C. fasciata* to identify the subspecies from the interior of southern Oregon.

Methods

I examined 319 adult *C. fasciata* (numbers of specimens in parentheses), including all known specimens from interior Oregon from southern Douglas (3), Josephine (3), Jackson (6), and Klamath (2) counties, and examples from northern interior California from Siskiyou (5), Trinity (18), Shasta (23), and Tehama (17) counties (Fig. 1) and from other localities from interior California (93). I also examined specimens of *phaea* (27), *rufula* (31), *intermedia* (48), and nominate *fasciata* (42). I excluded *canicauda.*

Specimens were compared for variation

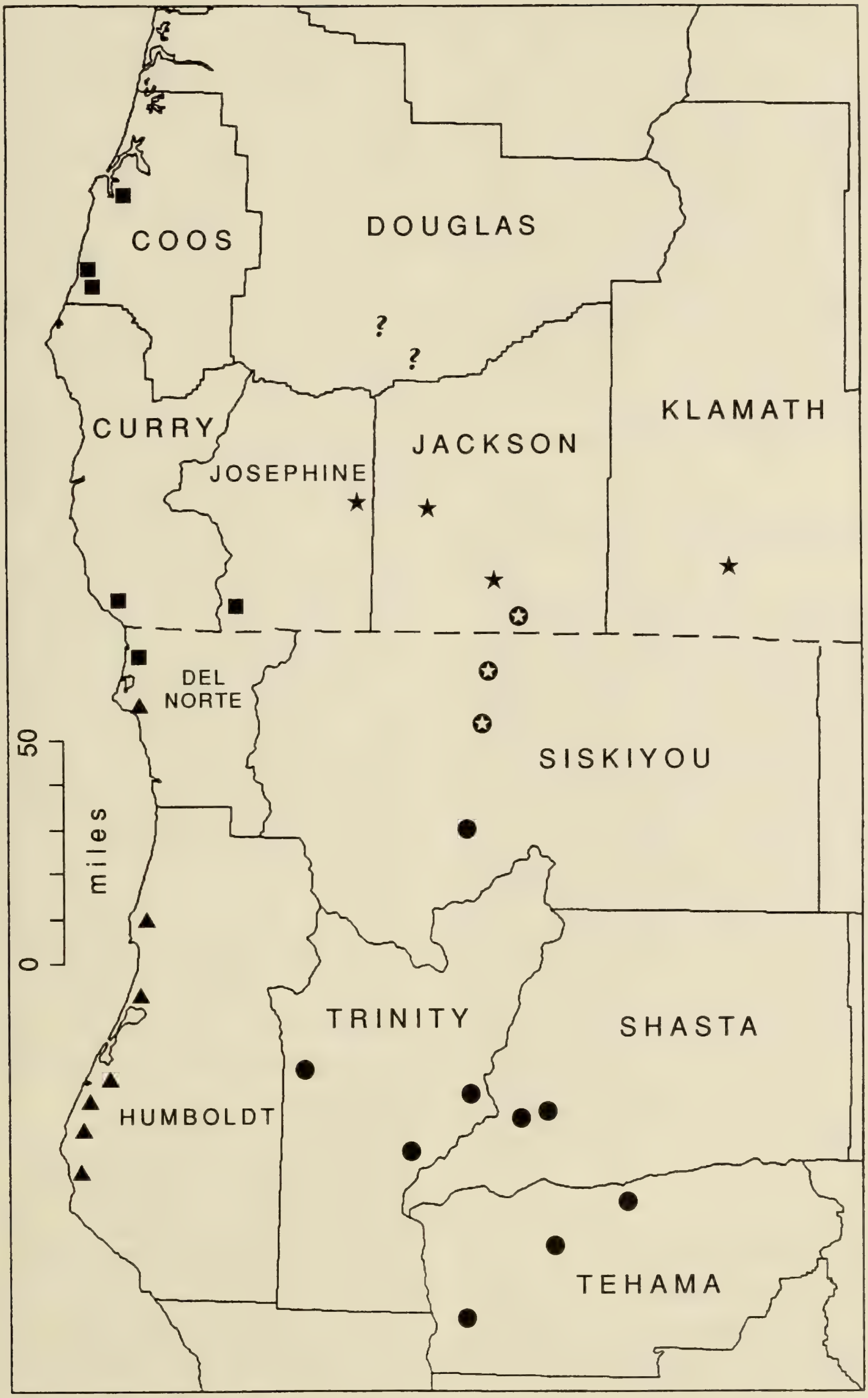

Fig. 1. Localities of specimens examined of *Chamaea fasciata* subspecies from southern Oregon and northern California: *phaea* (■), *rufula* (▲), *margra* (★), *henshawi* (●), *margra* × *henshawi* (✪), and subspecies unknown (?).

Table 1.—Tail lengths of adult male *Chamaea fasciata.*

Subspecies[a]	*n*	Range	Mean	*SD*
phaea	11	73.9–83.0	78.8	2.88
margra	4	73.7–83.0	78.2	
henshawi[b]	15	76.8–88.8	81.2	3.70
rufula[c]	13	76.9–84.6	80.0	2.35
intermedia	11	79.7–88.4	85.6	2.38
fasciata[d]	6	79.6–86.3	84.0	

[a] Specimens from entire range unless otherwise indicated.

[b] Specimens from northern interior California.

[c] Seven specimens from northern coastal California and six from Marin County, California.

[d] Specimens from Monterey County, California.

in plumage color and size. Tail lengths of males with unworn rectrices were compared (Table 1). Tail length of females averages shorter than males in populations from central California (Bowers 1960). Too few females were available in this study for meaningful comparisons. Preliminary analyses of other standard measurements of specimens from Oregon and northern California show no geographic variation. Plumages of males and females are alike in color (Bowers 1960, Pyle et al. 1987), and sexes were combined in making comparisons. Plumage colors were determined from specimens collected in fall and winter. Capitalized names of colors are from Ridgway (1912) and their nearest available equivalents following a slash (/) are from Smithe (1975), with my modification in lower case. Abbreviations of museums are given in the acknowledgments.

Geographic Variation

Specimens from coastal Oregon, northwestern coastal California, and northern interior California are characterized as follows:

Tail length.—There is minor geographic variation in tail lengths of males (Table 1). Males from coastal Oregon average only 2.4 mm smaller than birds from interior California; 18% of the Oregon birds have shorter tails than those from California and 33% of the California birds are longer than those from Oregon. Tail length of males from central coastal California (e.g., nominate *fasciata* and *intermedia*) average longer than others from California and Oregon (Table 1); 82% of the central coastal California birds have longer tails than those from Oregon.

Crown color.—The crowns of specimens from coastal Oregon are darker (near Clove Brown/Fuscous) and browner (less grayish) than the brownish-Mouse Gray/brownish Glaucous of interior California populations. The crowns of birds from northwestern coastal California are usually slightly paler than in the coastal Oregon populations.

Back and upper tail coverts.—The back and upper tail coverts of specimens from coastal Oregon and Del Norte and Humboldt counties in northwestern coastal California are darker and more reddish-brown (near Warm Sepia/Burnt Umber) than birds from other populations. Compared to the coastal populations, birds from the remainder of northwestern California, including worn specimens, are browner (less reddish). Specimens from the interior of northern California are pale, averaging near Hair Brown/Drab, and range in color from grayish-brown to brown. Birds from extreme northern Siskiyou Co., California (Hornbrook, Yreka), are slightly darker and browner than other specimens from interior California.

Lower parts.—The color of the upper and lower breast is slightly darker and more reddish (near Fawn Color) in specimens from coastal Oregon than in birds from northwestern California. Specimens from interior northern California are much paler below than are coastal populations. Birds from Trinity and Shasta counties average darker (near Pale Vinaceous Pink) below than those from Tehama Co. (Light Pinkish Cinnamon to Pinkish Buff/pale Flesh Color); those from farther south average even paler below.

Flanks and under tail coverts.—The color of the flanks and under tail coverts is browner (less gray) in northern coastal specimens (pale Natal Brown/Russet) than in interior California birds. However, the flanks of birds from extreme northern Siskiyou Co. are browner than those of specimens from elsewhere in interior California.

Taxonomic Status of the Southern Oregon Populations

Although there is considerable individual variation in interior California populations, there is also clinal variation in color. Birds from northern interior California are browner (less gray) above and are darker pink below than those from farther south. Specimens from Hornbrook and Yreka, Siskiyou Co., in northern interior California are intermediate between examples of *henshawi* and new and older specimens from the Rogue River Valley in Jackson and Josephine counties, Oregon. Birds from the Rogue River Valley are isolated geographically (Fig. 1) and ecologically from the northern interior California populations and differ consistently from them in the color of the upper and lower parts. The population is here named

Chamaea fasciata margra, new subspecies

Holotype.—USNM 597165 (formerly SOC 1441), adult, sex ?, Perozzi Acres south of Southern Oregon State College campus, Ashland, Jackson Co., Oregon, collected 29 Apr 1984 by M. Gould.

Diagnosis.—Both sexes of the new subspecies are identical in plumage color, and are noticeably browner (Bister/dark Raw Umber) and less grayish above than *henshawi* from central Siskiyou, Trinity, Shasta, and Tehama counties, California, and less reddish-brown above than *phaea* and *rufula*. Below, *margra* is paler (Pinkish Cinnamon/very pale Flesh Color) than *phaea* and is more pinkish (less whitish) than *henshawi*. The flanks and undertail coverts are browner (Wood Brown) than in *phaea* and less grayish than in *henshawi*. The colors of the cheek and crown are closer to *phaea* than to *henshawi*. The new subspecies resembles the geographically distant nominate *fasciata* in the colors of the back, upper tail coverts, breast, throat, and flanks, but differs in having a dark brownish-gray (not chocolate brown) crown and less pinkish undertail coverts. Compared to *intermedia*, specimens of *margra* collected in March have slightly grayer (less brownish) flanks and birds collected in the fall are paler brown above. Tail length averages shorter in adult male *margra* than other subspecies (Table 1).

Distribution.—Rogue River Valley in Jackson and eastern Josephine counties, Oregon.

Paratypes.—Josephine Co.: SD 24468, female, Grants Pass, 10 Dec 1918; OSU 4489, 4490, 4491, males, Gold Hill, 24, 28, 29 Mar 1916.

Etymology.—The name *margra* is a combination of Marvin and Grace (Browning), my parents, who made it possible for me to name the subspecies.

Remarks.—A specimen from Louse Creek near Grants Pass that was thought to be in the Carnegie Museum (Gabrielson & Jewett 1940) could not be located. A male and female (SD) from Klamath Falls, Klamath Co. (Phillips 1986), collected 7 November 1912, with tail lengths of 80.0 and 78.1 mm, respectively, are slightly paler above than *intermedia* and are definitely darker above and below than *henshawi*. I tentatively assign the two to *margra*. A worn specimen (CAS) from Siskiyou, in southern Jackson Co., Oregon, is similar to *margra* below but is slightly grayer above. Two worn specimens (CAS) from Hornbrook in northern Siskiyou Co., California, are similar below and are slightly grayer than the Siskiyou, Oregon specimen. I consider the specimens as *margra*>*henshawi*. Another intergrade, an adult (CAS) from Yreka, California, only about 12 miles south of Hornbrook, has a pale (nearly white) lower belly similar to most specimens of *henshawi* but it is otherwise within the range of variation in *margra.* A relatively unworn female (SOC) from 9 miles west and 4 miles south of O'Brien (about 40 miles SW of Grants Pass), Josephine Co., Oregon, collected 22 July 1960, is referable to *phaea.*

Gullion (1948) found a small colony of Wrentits 5 miles northwest of Roseburg in the Umpqua River watershed, Douglas Co., in April 1947. He described two birds as "somewhat grayer and lighter" than *phaea,* and stated that the birds "undoubtedly" represent *henshawi.* Although the A.O.U. (1957), apparently following Gullion (1948), listed Roseburg as the northern limit of the breeding range of *henshawi,* there are no specimens from that locality; the A.O.U. (1983) did not include interior Oregon in the range of the species *C. fasciata.* Three specimens collected south of Roseburg in Douglas Co. (Fig. 1) are definitely darker and browner than *henshawi.* A specimen (SD) from 3 miles southeast of Canyonville (=20 miles south of Roseburg), collected 1 October 1987, is dorsally darker brown than *margra* and less reddish than *phaea,* and is paler ventrally than either subspecies. Two worn individuals (USNM) from the former town of Anchor (about 10 miles east of Azalea; 28 miles south of Roseburg), collected 7 August 1916, are similar to worn individuals of *phaea.* I prefer not to assign the specimens from Douglas Co. to a subspecies until additional material becomes available.

Discussion

The Rogue River Valley is unique vegetationally and is drier and hotter than other regions of western Oregon (Detling 1961, Franklin & Dyrness 1973). The chaparral habitat (*Ceanothus cuneatus* and *Arctostaphylos* sp.) in the Valley during July averages cooler and wetter than in Siskiyou Co., California (Detling 1961). Morphological characteristics of some species of birds from the Valley differ from the remainder of Oregon, and are similar to populations from northern interior California. Subspecies in *Parus inornatus* and *Pipilo fuscus,* both described from specimens from the Valley, also occur in northern interior California. The third such example is *Chamea fasciata margra.*

Populations of *C. fasciata* are sedentary, although immatures may move upslope in summer (Verner et al. 1980). Bowers (1960) concluded that the sedentary habit in the species results in slow transmission of genetic characters. He reported steep gradients in color between some populations of *C. fasciata* from central-western California, with dark birds occurring in regions of dense vegetation and high humidity; pale birds were from regions of less dense vegetation and lower humidity. Birds that differ in color were sometimes separated by relatively short geographic distances (20 to 40 miles) and small ecological differences (Bowers 1960).

The distance between the southern range of *margra* and the northern range of *henshawi* is likewise short, and differences in climate are small. These two populations are also separated by the Siskiyou Mountains. Balds of chaparral occur on the drier and eastern slopes of these mountains, with coniferous forests on the western and northern slopes. The population from the Rogue River Valley is also disjunct from other populations from Oregon (Fig. 1).

The postglacial distribution of chaparral once extended to the Columbia River but the habitat became restricted to the Rogue and Umpqua river valleys with increasing precipitation and decreasing temperature (Detling 1961). Colonization by *C. fasciata* of the Rogue River Valley was perhaps from individuals moving up the Siskiyou Mountains via isolated balds of *Ceonothus* that occur on the drier eastern and southern exposures, and crossing coniferous forests of the northern and western slopes to the Valley floor.

Gabrielson (1931) reported Wrentits from three localities in the Rogue River Valley, but Gabrielson & Jewett (1940) and Browning (1975) regarded the species as uncommon there. Wrentits are now fairly common in the region, are regularly reported on Christmas Bird Counts in Roseburg, and in the last decade the species has been reported in interior Oregon as far north as the Columbia River at Portland. The species is not known north of the Columbia River (contra Root 1988). Deforestation, fires (also opening some regions to chaparral [Franklin & Dyrness 1973]), and concurrent global warming may be contributing to increased habitat for *C. fasciata*. Because variation in color in the species is a response to climate and vegetation (Bowers, 1960), studies of geographic variation in the northern parts of the range are desirable.

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THE GENERIC NAME FOR CRESTED CARACARAS (AVES: FALCONIDAE)

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Abstract.—The generic name *Polyborus* Vieillot, 1816, is based on a type species of uncertain identity, the Caracara of Buffon, ultimately of Marcgrave, and must be replaced by *Caracara* Merrem, 1826. *Falco brasiliensis* Gmelin, 1788, is also based on the Caracara of Marcgrave and thus is also not of certain identity, and *brasiliensis* cannot replace *buffoni* in the present combination *Circus buffoni* (Gmelin) as some authors have proposed.

Three nominal species of crested caracaras, *plancus* Miller, *cheriway* Jacquin, and *lutosus* Ridgway, were carried in the genus *Polyborus* Vieillot without question for about a century after Kaup (1847) fixed the limits of that genus. Hellmayr & Conover (1949), acting on information provided by Schneider (1938) concerning the identity of the type species of *Polyborus,* replaced that familiar name with *Caracara* Merrem. Amadon (1954) attempted to show that the change was unnecessary and that *Polyborus* should be used. *Caracara* was used by the American Ornithologists' Union [A.O.U.] (1957), Wetmore (1965) and Blake (1977), but *Polyborus* has been used most recently (Stresemann & Amadon 1979, A.O.U. 1983, Sibley & Monroe 1990).

The population of the Crested Caracara in Florida, under the name *Polyborus plancus audubonii,* is listed as Threatened under the Endangered Species Act. The taxonomic as well as the population status of any species so listed, and thus subject to permit regulations, must be understood to avoid confusion and oversight in protective efforts. This study is part of our continuing review of species limits in the genus. We studied the nomenclatural history of these caracaras to determine whether the use of *Polyborus* can be sustained, and concluded that it cannot. A review of that history is necessary to support our conclusion. That same review sheds light on the proper use of the name *Circus buffoni* for the Long-winged Harrier of South America, for which *C. brasiliensis* was recommended by Schneider (1938) and Hellmayr & Conover (1949).

History

Gmelin (1788:254, 257) listed the names of three taxa now associated with the crested caracaras—*plancus* Miller, *tharus* Molina, and *cheriway* Jacquin—along with several species of eagles in the Linnaean genus *Falco,* which included all diurnal birds of prey. In the part of *Falco* in which he listed kites, Gmelin (1788:262) coined the name *brasiliensis,* giving as references works by Brisson, Ray, Buffon, Willughby, and Latham, with the locality "Brasilia." Farther in the genus *Falco,* where present-day harriers were listed, Gmelin (1788:277) first used the name *buffoni,* giving as a basis Latham's (1781) Cayenne Ringtail and a locality of "Cayenna."

Latham (1790) listed *plancus, cheriway,* and *tharus* in the genus *Vulture,* but followed Gmelin (1788) in listing *brasiliensis* as a species of *Falco* with kites. He listed *buffoni* as a form of *Falco cyaneus,* a harrier. Latham later (1801) moved *tharus* to *Falco,* listing it among the eagles. Shaw (1809) similarly treated *plancus* and *cheriway* as vultures, *tharus* as a falcon, and *buffoni* as a harrier. In the section of *Falco* that included kites, Shaw (1809:106) gave the vernacular "Caracara Kite" for *Falco brasiliensis* of Latham (and Gmelin) and referred to it as the "Brasilian Kite called *Caracara*" of Wilughby.

Vieillot (1816a) used the vernacular name Caracara and established the generic name *Polyborus.* Parts of the written description of *Polyborus* (face bare, claws blunt) apply to the crested caracaras, but other parts are not distinctive. The only species listed in the genus, which becomes the type species by monotypy, was "Caracara, Buff." Vieillot (1816b) again used the generic name (spelled *Poliborus*) in the same sense, noting it was in the Order Accipitres and the family of vultures, but with a more complete description apparently taken in part from Azara and a living bird. Vieillot (1816b) proposed the name *Polyborus vulgaris* for "*Falco brasiliensis,* Lath.," presumably Latham (1790) where the listing is based at least in part on Gmelin (1788:262). The name *vulgaris* Vieillot is automatically a junior synonym of *F. brasiliensis* Gmelin.

Vigors (1824) used Vieillot's name *Polyborus* for a genus of eagles, stating that "The type of the genus is the *F. braziliensis* [sic] of Linnaeus [=Gmelin], the *Caracara* of M. Buffon." Vigors did not include the species now called crested caracaras in the eagles or elsewhere in his Falconidae, probably leaving them with the vultures, not treated in that work. Kaup (1847) first used *Polyborus* in a modern sense, listing as species *vulgaris, cheriway, plancus,* and *tharus,* as well as *F. braziliensis* [sic] Gm. Thus he was apparently also the first to indicate a relationship among the forms now considered by some to be a single species. However, Kaup listed the names in several ways, rendering his intentions obscure. Bonaparte (1850) listed *tharus, cheriway, plancus,* and *vulgaris* all as synonyms of *brasiliensis* Gm.

Strickland (1855) was the first to provide a modern synonymy of *Polyborus,* giving priority to Molina's *tharus* and placing *brasiliensis* and the other names under it. There is no mention in this synonymy of the "Caracara Buff." cited by Vieillot (1816a) in his initial use of *Polyborus,* but "Caracara *Marcgr.* Hist. Bras. p. 211" is included. Because Marcgrave's (1648) caracara was the basis for Buffon, Brisson and others cited by Gmelin (1788) in naming *brasiliensis,* the stage was laid for Ridgway (1875), in the first monographic treatment of the genus, to list the type species as "*Falco brasiliensis* Gmel. = *P. tharus* (Mol.)." Later works recognized the priority of *plancus* over *tharus,* and the equation is now given as "'Caracara' Buffon = *Falco plancus* Miller" (e.g., A.O.U. 1983). The fact that Marcgrave's writing was about Brasil enabled Wetmore (1926) to retain the name *brasiliensis* for the northerly subspecies when the considerable variation in birds south of the Amazon was formally recognized.

Schneider (1938) studied the unpublished original paintings and watercolors of Marcgrave and attempted to match them with the published woodcuts (Marcgrave 1648). He determined that Marcgrave's caracara, *Falco brasiliensis* of Gmelin 1788:262, was based on a painting which he identified as being of a harrier ("Weihe"), which he further equated with *Falco buffoni* Gmelin 1788:277. Thus *brasiliensis,* by virtue of page priority, becomes a senior synonym of *Circus buffoni,* used for the Long-winged Harrier, and should replace it. According to Schneider (1938), Vieillot's *vulgaris* should then be used for the subspecies of *plancus* to which *brasiliensis* had been applied.

Hellmayr & Conover (1949) accepted Schneider's determination and conclusions, and further pointed out that because the Caracara of Buffon was the type species of *Polyborus* that name followed it and became a synonym of *Circus,* thus becoming unavailable for caracaras. They proposed that *Caracara* Merrem, with the type species *Falco plancus* Miller, be used for the genus of crested caracaras.

Amadon (1954) stated that Schneider's proposed replacement of *buffoni* with *brasiliensis* on the basis of page priority was not allowed under the International Code of Zoological Nomenclature. The action is contrary to Recommendation 24A, which suggests that a first reviser should act in such a way as to preserve stability of nomenclature. Recommendations are not binding, and Schneider (1938), clearly acting as first reviser, should be followed if the basis for his action is correct. Amadon (1954) quoted a communication from E. Stresemann who expressed doubt as to Schneider's identification and "would prefer to declare the drawing [of Marcgrave] as unidentifiable. In this way the name *Circus buffoni* will be retained for the Long-winged Harrier." Although apparently accepting the idea that Marcgrave's drawing be considered unidentifiable, Amadon insisted that it "may, indeed, be of a caracara, which is what Marcgrave called it." Amadon (1954) went on to suggest that "under these circumstances the diagnosis sustains the name" and that *Polyborus* should be retained. We reject the concept that a drawing can be considered unidentifiable as a matter of preference, to sustain a name, and further that it can be unidentifiable for one purpose but identifiable for another. Additionally, the concept that the diagnosis can sustain a generic name if it does not agree with the type species is not in accord with the Code.

Discussion

Because Marcgrave (1648) was the acknowledged basis for all the references cited for *Falco brasiliensis* by Gmelin (1788), the identity of the name does depend on the identification of the bird that was illustrated and described by Marcgrave. First, we express our opinion that the identification must be based on what Marcgrave published rather than on a painting or watercolor that may or may not have served as the basis for the published illustration, particularly as Marcgrave did not refer to any such source. But even if the painting should be considered definitive, we are not certain that Schneider (1938) matched the right painting with the woodcut.

Many of the paintings (oil series A32–35, watercolor series A36–37) made by or for Marcgrave during his explorations in Brasil in 1638–1643 or 1644 are preserved in "Libri Picturati" at the Jagellonian Library in Kraków, Poland (Schneider 1938, Whitehead 1976, Browning 1989). Many of these have been labeled and collated with Marcgrave's published illustrations, but P. J. P. Whitehead (in litt., 1991) believes that misidentifications occurred in the labelling. There are three possibilities for the source of Marcgrave's woodcut of the caracara. Painting "A 33, S. 209. b" was identified by Schneider (1938:93) as *Buteo magnirostris.* A transparency of that painting was obtained (at the senior author's request) by M. Ralph Browning in 1988, when he was working on the identity of a cormorant attributed to Marcgrave (Browning 1989). The transparency shows the words "Inaie" and "Caracara, Marc. p. 211–212" written above the painting. We agree that the bird illustrated is *Buteo magnirostris.* According to Schneider (1938) painting "A 33, S. 211" is missing. Marian Zwiercan, Deputy Director of the Jagellonian Library, has informed us (in litt. 14 Jan. 1988, 14 Mar. 1991) that on page 211 "only the name of the bird [Caracara] is written, but there is no picture" and probably there never was one on that page. Schneider (1938) reproduced a miniature watercolor ("A 36 S. 212") apparently also labeled as "Caracara" and identified it as a harrier and as the source for the published woodcut that accompanied Marcgrave's (1648) description of the caracara. The reasons for equating the two are not stated; in our opinion, the two illustrations differ markedly, particularly in the proportions of the wings and tail and in the representation of the claws and bill. We doubt that Schneider properly determined the source of the woodcut. Further, we doubt that the woodcut (Fig. 1) can be identified

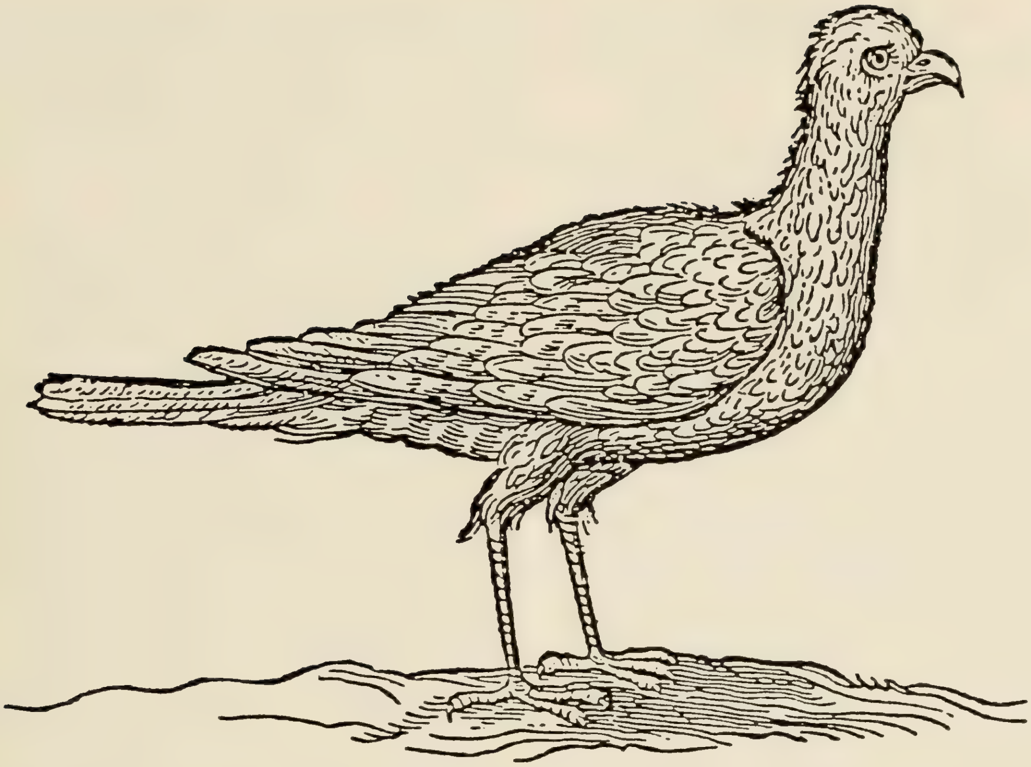

Fig. 1. Reproduction of the woodcut of the Caracara from Marcgrave (1648).

with certainty as any species of bird. It is a virtual caricature of a bird of prey.

Marcgrave (1648:211–212) indicated that caracara was a native name, and used the Portugese word "Gaviaon" (sparrowhawk) for it. He noted that it is the size of a kite ("milhafre") and that the wings do not reach the end of the tail. Also, he said that the head and feet are like a vulture ("abutre") and that the claws are highly curved ("semilunares"), very sharp ("agudissimas") and long. Further, he reported that there is a form of the same size and color but with the breast and abdomen white. Significantly, we believe, he did not mention a crest on the head. As a behavioral character, he noted that the bird is "prejudicial" toward chickens. We have omitted his mention of size because we do not know how his units of measurement ("dedos," or fingers) convert to modern units, and of color because the plumage color is not distinctive.

Marcgrave clearly demonstrated different concepts of hawks, kites, and vultures. Features of this description that suggest a caracara are the proportions of the wing and tail and the vulture-like head. Features that tend to eliminate the caracara are the curvature and sharpness of the claws and the indication of a dimorphism. The latter do, in fact, suggest the Long-winged Harrier, but the characters that suggest caracara tend to negate that species. The description, almost certainly based on an immature bird, may be a composite, and we cannot with certainty state that it is of either a caracara or a harrier.

Gmelin (1788) did not refer directly to Marcgrave, but to others who interpreted Marcgrave's description. Willughby (Ray 1678) listed the bird as "The Brasilian Kite called Caracara . . ." and gave a translation of Marcgrave's text. He translated the units of measurement directly to inches (tail 9, wing 14) and repeated that the wings do not reach the end of the tail. Rather than our translation of "abutre" as "vulture," Willughby said "it hath a Hawks Head" and "Hawks Feet." He repeated the mention of "semicircular, long, sharp, black Talons" and concludes "For the bigness, colour, and preying upon Poultry, we have subjoyned this to the *Kites* not withstanding *Marggravius* maketh it a kind of *Nisus* or *Sparrowhawk*."

Brisson (1763) listed the species as "Circus Brasiliensis" (Brissonian specific names are not available by decision of the International Commission of Zoological Nomenclature) and uses the vernacular "Le Busard [buzzard] du Bresil." He did not characterize the head, but noted the "acutissimi" claws.

Buffon (1770) repeated the essentials of Marcgrave's description but, like Willughby, described the head and feet as hawk-like rather than vulture-like. He added that the claws were like those of a sparrowhawk ("espervier") and emphasized their length and sharpness ("tres-aigus").

Latham (1781), with the name "Brasilian Kite," gave only a partial description, omitting the nature of the head and feet and the sharpness of the claws. He differed from others in stating that the "wings reach to near the end of the tail" and notes that there was no mention whether the tail was forked. Significantly, perhaps, Latham (1781) separated his Brasilian Kite (p. 63, no. 47) far from both the Plaintive Eagle (*Falco plancus* Miller) (p. 34, no. 9) and the Cayenne Ringtail (p. 91, no. 76A), which formed the basis for Gmelin's (1788) *Falco buffoni,* in his listing of the genus *Falco.*

The similarities in the descriptions quoted may result from sequential translations of Marcgrave's text. It is possible, however, that Brisson and Buffon translated from Willughby rather than directly from Marcgrave. Regardless of what Marcgrave had in mind when he described his caracara, it seems certain that none of those authorities cited by Gmelin had anything in mind that resembled what we now call caracaras. It is perhaps even uncertain what Vieillot (1816a) had in mind when he listed "Caracara, Buff.," without a date or specific reference, as a species in his genus *Polyborus.* Buffon (1771) also used the name "Le Caracara" for what is now *Psophia crepitans.* The word "caracara" apparently meant different kinds of birds to different groups of native people, a fact that may have confused both Marcgrave and Vieillot.

Conclusion

We conclude that Marcgrave's illustration and description of the caracara, and by extension Gmelin's *Falco brasiliensis,* cannot definitely be identified, and that the latter can have no standing as a primary name or synonym in ornithological nomenclature. It cannot replace Gmelin's *Falco buffoni,* first applied to the Long-winged Harrier of South America by Berlepsh (1908). Vieillot's genus *Polyborus,* based on an unidentifiable species, can have no standing and we accept *Caracara* Merrem, type species *Falco plancus* Miller, as the generic name for the Crested Caracaras (with the nominal species *plancus, cheriway,* and *lutosus*) as recommended by Hellmayr & Conover (1949).

Acknowledgments

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A NEW CHINESE EYED TURTLE OF THE GENUS *SACALIA* (BATAGURINAE: TESTUDINES)

John B. Iverson and William P. McCord

Abstract.—A new species of batagurine turtle, *Sacalia pseudocellata,* is described from Hainan Island, China. Similar to and apparently sympatric with *Sacalia quadriocellata,* it differs from that species and *S. bealei* by having eyelike markings without "pupils" on the posterolateral aspect of the head, a slightly tricarinate (generally unicarinate in *S. bealei* and *S. quadriocellata*) and wider carapace, more extensive black plastral pigment, a more extensive plastron, longer and narrower gular scutes, and a shorter interfemoral seam.

Cistuda bealei (the four-eyed turtle) was first described in 1831 by John Edward Gray from "China," and it is known to range from southeastern China to at least central Vietnam (Buskirk 1989, Iverson 1992). Although it has been placed in four different genera by various authors, it was finally returned to Gray's (1870) monotypic genus *Sacalia* based on biochemical (Merkle 1975) and morphological studies (McDowell 1964).

In 1903 Siebenrock described the western geographic variant of *Sacalia* (then *Clemmys) bealei* as *C. b. quadriocellata.* This form was considered a separate species by a few early authors (e.g., Pope 1935, Bourret 1941); however, Sachsse (1975), Rödel (1985), and Rödel & Praedicow (1988) argued that *quadriocellata* is conspecific with *bealei.* Recently, Fu & Zhao (1989) presented morphometric and color pattern data that supported the recognition of *bealei* and *quadriocellata* as distinct species.

Three-"eyed" turtles from Hainan Island represent an undescribed species and they show more similarity with *Sacalia bealei* and with *S. quadriocellata* (with which it is apparently sympatric) than with any other Chinese batagurine turtles. This distinctive species is tentatively referred to the genus *Sacalia,* although confirmation of this assignment must await the availability of osteological material.

Sacalia pseudocellata, new species
Chinese false-eyed turtle
Fig. 1A–D

Holotype.—UF 81505, an adult male, preserved in alcohol; reported to have been collected between Tungfang [19°03′N, 108°56′E] and Kancheng [18°51′N, 108°37′E; ca. 48 km from Tungfang], western Hainan Island, China; purchased from local persons living between those cities by Mr. Oscar Shiu, in the spring of 1988.

Paratype.—UF 81506, an adult female, preserved in alcohol; same data as holotype, except purchased in the spring of 1990.

Diagnosis.—A medium-sized species of *Sacalia* (Fig. 1A–D, Table 1) with black-bordered yellow to olive-green blotches dorsolaterally on head region, a weakly tricarinate carapace (generally unicarinate in other *Sacalia*; e.g., *S. bealei* and *S. quadriocellata*), a carapace of medium width (relatively narrow in other *Sacalia*), heavily pigmented plastron (lightly pigmented in other *Sacalia*), a relatively long, broad plastron (shorter and narrower in other *Sacalia*), a relatively long, narrow gular scute (shorter and wider in other *Sacalia*), a relatively long interpectoral seam (shorter in other *Sacalia*), and a relatively short interfemoral seam (shorter in other *Sacalia*).

Description (based on the types, and a living juvenile female).—Carapace length (CL)

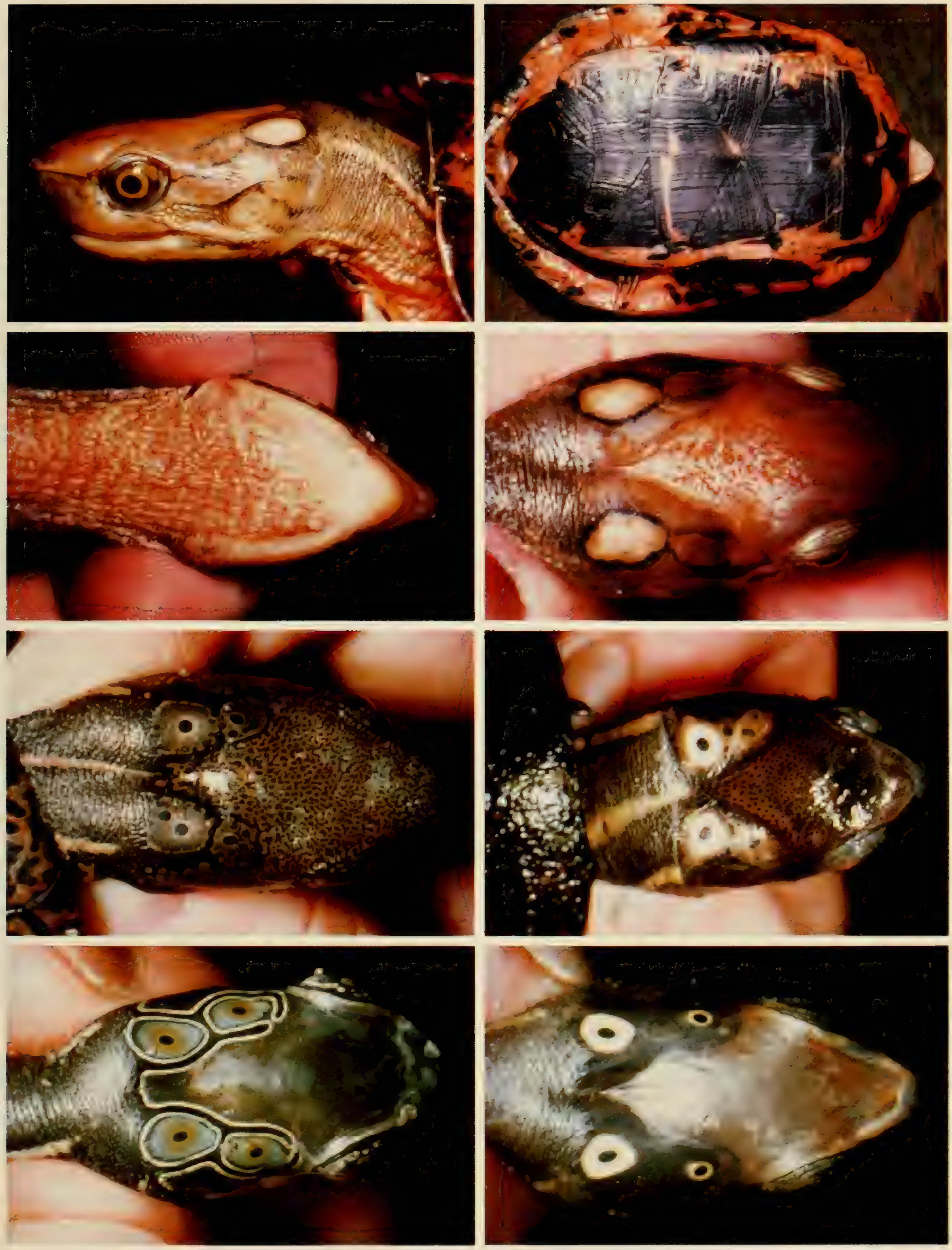

Fig. 1. Adult female *Sacalia pseudocellata* (A–D; paratype: UF 81506; 176 mm carapace length) from Hainan Island, China; typical head patterns of male (left) and female (right) *Sacalia bealei* (E, F) and *S. quadriocellata* (G, H).

Table 1.—Morphometric characters useful in discriminating among species of the genus *Sacalia*. Character abbreviations are interhumeral seam length (IH), interpectoral seam length (IP), interfemoral seam length (IF), maximum gular scute length (GL), maximum gular scute width (GW), maximum carapace width (MCW), and anterior width of plastral hindlobe (PW3).

Sample	Sex	*n*	Carapace length (mm)	IH/IP	IF/PW3
S. pseudocellata	M	1	151.8	0.434	0.248
	F	2	147.8 (119–176)	0.255 (0.24–0.27)	0.255 (0.24–0.27)
S. bealei	M	5	127.2 (114–136)	0.609 (0.54–0.68)	0.310 (0.29–0.35)
	F	4	132.0 (119–140)	0.521 (0.42–0.69)	0.321 (0.29–0.38)
S. quadriocellata	M	4	127.0 (120–143)	0.677 (0.53–0.82)	0.339 (0.27–0.44)
	F	4	130.6 (127–139)	0.596 (0.48–0.70)	0.339 (0.29–0.38)

to at least 152 mm in males and at least 176 mm in females; carapace elliptical, weakly tricarinate (shell height at level of hinge/carapace length = CH/CL = 0.36 to 0.39; $\bar{X} = 0.375$), widest at level of marginal M7 (maximum carapace width: MCW/CL = 0.69 to 0.75; $\bar{X} = 0.721$), with a smooth to slightly serrated posterior margin, and with moderately obvious growth laminae.

M1, M7, M8, or M9 widest, M11 narrowest, and M9 tallest. Cervical scute small, basically rectangular (but widest posteriorly), and longer than wide. All vertebrals (V) wider than long; V1 contacting (or nearly so) seam between M1 and M2; V5 not contacting M10. Low medial keel most pronounced on V1, V4 and V5. Carapace dark to rusty brown, with tiny black flecks and streaks anteriorly.

Maximum plastron length shorter than carapace length (PL/CL = 0.93 to 0.95), slightly upturned anteriorly, with no hinge between pectoral and abdominal scutes. Anterior plastral lobe shorter than posterior lobe. Plastral forelobe width (across level of junction of humero-pectoral seam and lateral plastral margin) relatively wide (PW1/CL = 0.44 to 0.45; $\bar{X} = 0.445$). Plastral hindlobe width (at lateral junction of abdominal-femoral seam) relatively wide (PW3/CL = 0.51 to 0.53; $\bar{X} = 0.518$). Plastral hindlobe with shallow anal notch. Bridge moderately long (BL/CL = 0.35 to 0.37; $\bar{X} = 0.355$); a single small axillary and inguinal scute on each side of bridge. Average plastral formula: interpectoral seam (IP) $\geq$ interabdominal seam (IAB) > interanal seam (IAN) $\gg$ intergular seam (IG) > interfemoral seam (IF) $\gg$ interhumeral seam (IH). IG/IAB = 0.53 to 0.67 ($\bar{X} = 0.62$); IF/IAN = 0.70 to 0.78 ($\bar{X} = 0.73$); IG/IP = 0.55 to 0.63 ($\bar{X} = 0.59$). Interanal seam present and complete. Plastron yellow or orange, with black pigment covering most of each plastral scute (Fig. 1), although at least the margins of each scute marked with yellow; bridge marked with a longitudinal black stripe, primarily on the pectoral and abdominal scutes.

Head narrow; upper jaw not hooked; very small tubercles present dorsal to angle of jaw and anterior to tympanum. Dorsum uniform yellow to olive green. Dorsolateral head region with black-bordered longitudinal yellow to olive-green blotch, interrupted posteriorly, but continuing on neck to its base as a separate narrow black-bordered stripe; blotch may be divided in two distinct ocelli (single female; Fig. 1B, C), hourglass shaped (single juvenile female), or unconstricted (single adult male). Side of head with similar black-bordered longitudinal blotch immediately behind eye, continuous with anterior portion of dorsolateral blotch in juvenile and male. Dorsum of neck dark brown to black, with medial dark black-bordered salmon to orange stripe. Chin and tomia unmarked yellow; bottom of neck yellow anteriorly and orange or

Table 1.—Extended.

IP/MCW	GW/GL
0.328	1.893
0.335 (0.32–0.35)	1.378 (1.27–1.49)
0.238 (0.20–0.27)	2.191 (1.70–2.55)
0.281 (0.26–0.31)	2.269 (1.99–2.42)
0.212 (0.18–0.24)	2.417 (2.05–3.02)
0.219 (0.20–0.23)	2.286 (1.88–2.75)

salmon posteriorly, with vague black mottling. Triturating surfaces narrow and unridged.

Anterior surface of antebrachium covered with large, imbricate scales, the largest three or four of which are sickle-shaped; largest scales on hindlimb at heel, but much smaller than largest forelimb scales. Upper parts of limbs and tail finely scaled. Exposed parts of limbs dark olive green laterally, but immaculate orange or salmon ventrally; bottom of hindfeet also salmon to orange. Recessed areas of skin salmon to orange. Tail salmon ventrally, and dark olive brown dorsally, with a vague lighter dorsolateral line on each side. Male with larger, thicker tail than females; vent at level of carapace margin in male, anterior to it in females.

Etymology.—In reference to the lack of black "pupils" in the eye-like markings on its neck, we name this distinctive species *Sacalia pseudocellata.* The unusual mixture of Greek (*pseudo* for false) and Latin (*ocellata* for eyed) symbolizes the unusual combination of Chinese and American trade activities that have brought this new species to light.

Other material.—One juvenile female (topotypic) alive in the collection of William P. McCord (WPM); to be deposited on death in the UF collection.

Distribution.—Known only from the type locality.

Comparison with congeners.—Representative specimens (see Specimens examined) of *Sacalia bealei* and *S. quadriocellata* from public and private collections were measured (by JBI) and compared following the method of McCord & Iverson (1991). Discriminant function analysis (Fig. 2) of 13 character ratios (MCW/CL, CH/CL, MPL/CL, PW1/CL, PW3/CL, PW4/CL, GW/CL, MGL/CL, IH/CL, IP/CL, IAB/CL, IF/CL, and IAN/CL) revealed that *S. pseudocellata, S. bealei,* and *S. quadriocellata* are each morphometrically distinct. Specifically, *S. pseudocellata* is distinguished by its slightly wider carapace, its much larger plastron (both longer and with wider fore- and hindlobes), its longer and narrower gular scutes, and its slightly shorter interfemoral seam. That analysis also revealed several character ratios useful in discriminating among the three taxa (Table 1, Fig. 3).

Other taxonomic conclusions.—The discriminant function analysis also demonstrated conclusively that the syntypes of *Cistuda bealei* Gray are morphometrically identical to specimens from the Chinese mainland from Fujian and eastern Guangdong Provinces, China and from Hong Kong. A restriction of the type locality of *Sacalia bealei* to the Fuzhou region in Fujian Province, China (see also Pope 1929) seems justified, since *S. quadriocellata* apparently ranges from western Guangdong and eastern Guangxi provinces (Pope 1935) and Hainan Island (Schmidt 1927) westward to Vietnam (Siebenrock 1903) and Laos (Shiu, pers. comm.).

The discriminant function analysis also demonstrated that *S. bealei* and *S. quadriocellata* are distinct morphometrically, but bivariate plots of diagnostic characters revealed overlap in individual mensural characters (e.g., Fig. 3). However, of over 50 wildlife trade specimens of the two taxa that we have seen, none was intermediate in head color pattern (Fig. 1E–H). *Sacalia bealei* can be consistently distinguished from *S. quadriocellata* by the presence of black flecks on

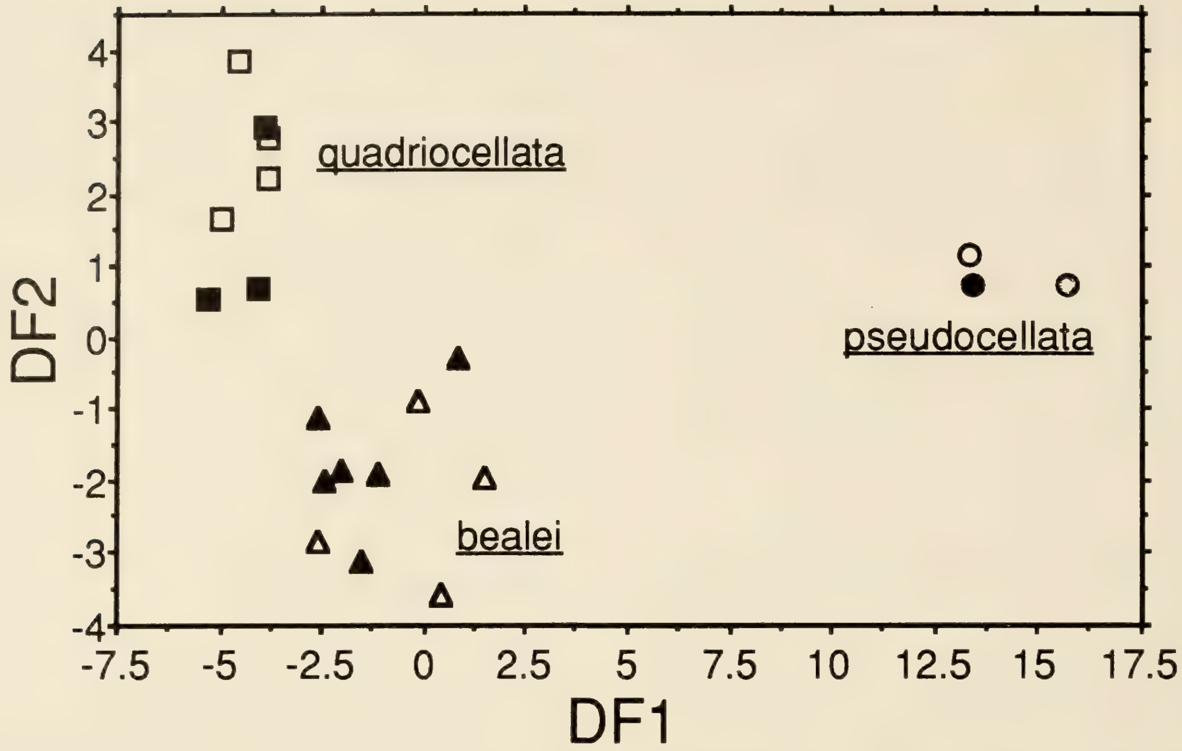

Fig. 2. Discriminant plot of combined analysis of male (solid symbols) and female (open symbols) *Sacalia* based on 13 characters (see text). First axis accounts for 91.4% of variation; second, 8.6%. Circles are *Sacalia pseudocellata*; triangles, *S. bealei*; and squares, *S. quadriocellata.*

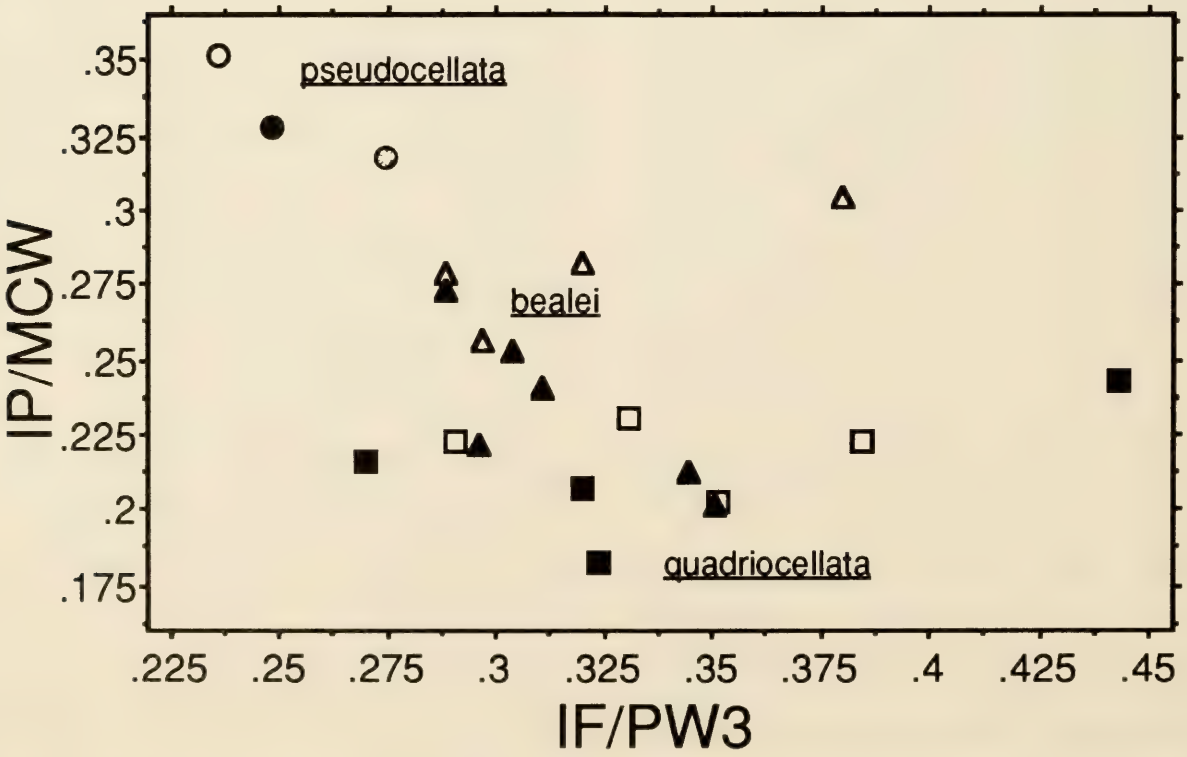

Fig. 3. Bivariate plot of the relationships among species of the genus *Sacalia* based on the characters IF/PW3 (interfemoral seam length/anterior width of plastral hindlobe) and IP/MCW (interpectoral seam length/maximum carapace width). Open symbols are females; solid, males. Species coded as in Fig. 2.

the anterior dorsum of the head of the former and the uniform unflecked dorsum in the latter (see also Pope 1935, and Fu & Zhao 1990). In addition, *S. quadriocellata* has four obvious ocelli on the posterior dorsum of the head, whereas *S. bealei* nearly always has much less obvious ocelli, with the posterior pair more obvious than the anterior pair (Fig. 1G, H). Thus, our data support Fu & Zhao (1990) in recognizing *S. bealei* and *S. quadriocellata* as separate species.

Specimens examined.—(See Acknowledgments for abbreviations) *S. pseudocellata*: China, Hainan Island (UF 81505–06; WMP 1, alive). *S. bealei*: China, mainland (AMNH 35179, 103735; BMNH 1947.3.4.33 and 1947.3.4.42; MCZ 58086 [formerly AMNH 34198]; MVZ 23936; UF uncat.; WPM 1–8 alive). *S. quadriocellata*: China, mainland (UF uncat.; WPM 1–8, alive); China, Hainan Island (AMNH 28337, 28339, 28341); and Laos (WPM 1–2 alive).

Key to the Genus *Sacalia*

1a. Blotches on dorsolateral aspect of head without distinct black "pupils"; plastron mostly black; carapace weakly tricarinate; interhumeral seam less than 45% of interpectoral seam length; interfemoral seam less than 28% of anterior width of plastral hindlobe . ... *S. pseudocellata*

b. Ocelli on dorsolateral aspect of head with distinct black "pupils"; plastron with small black blotches, streaks, or vermiculations; carapace unicarinate; interhumeral seam greater than 45% of interpectoral seam length; interfemoral seam greater than 28% of anterior width of plastral hindlobe 2

2a. Anterior dorsum of head finely spotted with black; anterior pair of ocelli on head much less obvious than posterior pair; interpectoral seam usually greater than 25% of maximum carapace width .. *S. bealei*

b. Dorsum of head uniform in color, unmarked with black; anterior pair of ocelli on head nearly or as obvious as posterior pair; interpectoral seam usually less than 25% of maximum carapace width .... *S. quadriocellata*

Acknowledgments

This species would not have been collected without the efforts of Oscar Shiu of Hong Kong. Curators and collection managers at the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), the Museum of Comparative Zoology at Harvard (MCZ), the Museum of Vertebrate Zoology at Berkeley (MVZ), and the Florida State Museum of Natural History (UF) facilitated specimen loans. D. R. Auth, J. R. Buskirk, M.-O. Rödel, and P. Grossmann provided literature, pertinent information, or other assistance. Support for Iverson was provided by Earlham College, the Joseph Moore Museum of Natural History, and his family.

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A NEW SUBSPECIES OF *CUORA GALBINIFRONS* (TESTUDINES: BATAGURINAE) FROM HAINAN ISLAND, CHINA

John B. Iverson and William P. McCord

Abstract.—A new subspecies of the Chinese box turtle, *Cuora galbinifrons,* is described from Hainan Island, China. It differs from other populations of this species by having a serrate posterior carapacial margin, a tricarinate carapace even in adults, mostly black pleural scutes streaked with lighter color, obvious growth laminae on the carapacial and plastral scutes even in adults, a relatively long interhumeral seam, an interanal seam 70–90% complete, and a dark-bordered elongated yellow blotch between the eye and tympanum.

Pope (1939:107) called the taxonomy of southeastern United States box turtles (genus *Terrapene*) "a quagmire, in which many a competent herpetologist has floundered and amateurs have expired with scarcely a struggle." This description could be equally well applied to the box turtles of the genus *Cuora* (including *Cistoclemmys*) of southeastern Asia. Over the past decade nine new species or subspecies of this genus have been described (Song 1984; Ernst & McCord 1987; Luo & Zong 1988; Ernst 1988a, 1988b; Ernst & Lovich 1990; Zhao *in* Zhao et al. 1990; Rummler & Fritz 1991; McCord & Iverson 1991), and three taxa have been synonymized with other species (Zong & Pan 1989, McCord & Iverson 1991). In addition, *C. pallidicephala* (McCord & Iverson 1991) is apparently a junior synonym of *C. zhoui* (Zhao et al. 1990). Thus, although our understanding of the taxonomic relationships within this diverse genus are improving rapidly, at least one more distinctive Chinese species remains to be described and variation in another (*C. galbinifrons*) is still confused. This paper addresses the latter problem.

The Indochinese box turtle, *Cuora galbinifrons,* was described by Bourret (1939) on the basis of four types from "Bach-Ma [16°11′N/107°48′E] (Annam) . . . [and] . . . Linh-Cam [18°31′N/105°35′E] (HaTinh [18°21′N/105°55′E]), Nord Annam" in North Vietnam. Apparently unaware of Bourret's description (see Buskirk 1989), Li (1958) described *Cyclemus* [sic] *flavomarginatus hainanensis* from Dali (village) of Mt. Diaoluo, Linshui Co., Hainan Island, China. Li's taxon was redescribed and elevated to species status in the genus *Cuora* by Zhao (*in* Hu et al. 1975; see also Koshikawa 1982), who was also apparently unaware of Bourret's description of the very similar *C. galbinifrons.* Despite the inclusion of *C. hainanensis* as a separate species on most recent lists (e.g., Iverson 1986, Zhao 1986, King & Burke 1989, Ernst & Barbour 1989; but not McCord & Iverson 1991), we concur with Zhao (*in* Buskirk 1989) and Zong & Pan (1989) in considering it synonymous with *C. galbinifrons.*

Cuora galbinifrons (s. l.) is now known to range from Vietnam (Bourret 1939, 1941; Petzold 1963, 1965; Felix 1965), southwestern China (Guangxi Prov., Xiadong village [22°12′N/108°43′E], Qiu Prefecture; Liu and Zhang 1987, Buskirk 1989), and southeastern (Li 1958; location verified by Zhao, pers. comm. to J. R. Buskirk) and southwestern Hainan Island (Tungfang [19°03′N/108°56′E], Kancheng [18°51′N/108°37′E], and Huangliu [18°30′N/

108°46′E]; Weiss 1989). However, in 1988 Hong Kong animal dealer Oscar Shiu sent us several unique serrate-shelled "*C. galbinifrons*" from central Hainan Island (Fig. 1). Closer examination revealed several other distinctive morphological and color characters. In addition, discriminant function analysis of mensural data (method in McCord & Iverson 1991) from 29 specimens from Vietnam and western and central Hainan revealed that these turtles were morphometrically distinct as well (Figs. 2 and 3).

Drawing attention to the distinctive serrate rear margin of its carapace, we name this new form

Cuora galbinifrons serrata, new subspecies

Serrate Indochinese Box Turtle

Fig. 1, right

Holotype.—UF 81791, an adult male, preserved in alcohol; collected 100 km east of Tungfang at Tainhfien in central Hainan Island, China; purchased from local people by Mr. Oscar Shiu, in the summer of 1988.

Allotype.—USNM 314208, an adult female, preserved in alcohol; same data as holotype.

Paratypes.—UF 81792–97 (all in alcohol), one adult female, two adult males, two subadults (apparently females), and one yearling; and UF 81798 (complete skeleton), an adult male; all with same data as holotype.

Diagnosis.—A subspecies of *Cuora galbinifrons* with a serrate posterior carapacial margin (a smooth margin in all other populations); a distinctly tricarinate carapace even in adults (usually smooth to weakly tricarinate in others); mostly black pleural scutes streaked with lighter color (mostly light colored pleural scutes streaked with black in others); obvious growth laminae on the carapacial and plastral scutes even in adults (usually smooth, particularly on the plastron, in old adults in others); a plastron with abundant light pigment, never all black (variable, frequently all black in others); a gular scute that becomes slightly notched medially in large adults (almost never so notched in others); a relatively long interhumeral seam (mean, 42% of interpectoral seam length; 22% in other populations); an interanal seam 70–90% complete (usually absent in others); and a dark-bordered elongated yellow blotch between the eye and tympanum (blotch indistinct if present at all in others).

Description (based on all nine types).—Carapace length (CL) to at least 194 mm in males and at least 179 mm in females, shell elliptical, moderately tricarinate and domed (maximum shell height/CL = 0.42 to 0.48; mean = 0.46), widest at the level of marginal M7 or 8 (maximum carapace width/CL = 0.70 to 0.81; mean = 0.75), with a serrate posterior margin (even in the yearling), and with moderately obvious growth annuli. M1 longest; M7, 8, and 9 next longest, coequal; M11 smallest; M7 tallest; M3–5 and M8–12 distinctly flared. Cervical scute small, generally rectangular, but wider posteriorly than anteriorly, and longer than wide. Vertebrals V1–V5 wider than long; V1 not contacting M2; V5 not contacting M10. Medial keel least pronounced on V5; keel marked with black-bordered yellow to yellow-brown line. Lateral keels most pronounced on pleural P3; keels marked with narrow yellow to yellow-brown line bordered medially with black pigment. Carapace dark brown with black markings to nearly all black. Ventral surface of each marginal highly variable in color, from all black to mostly

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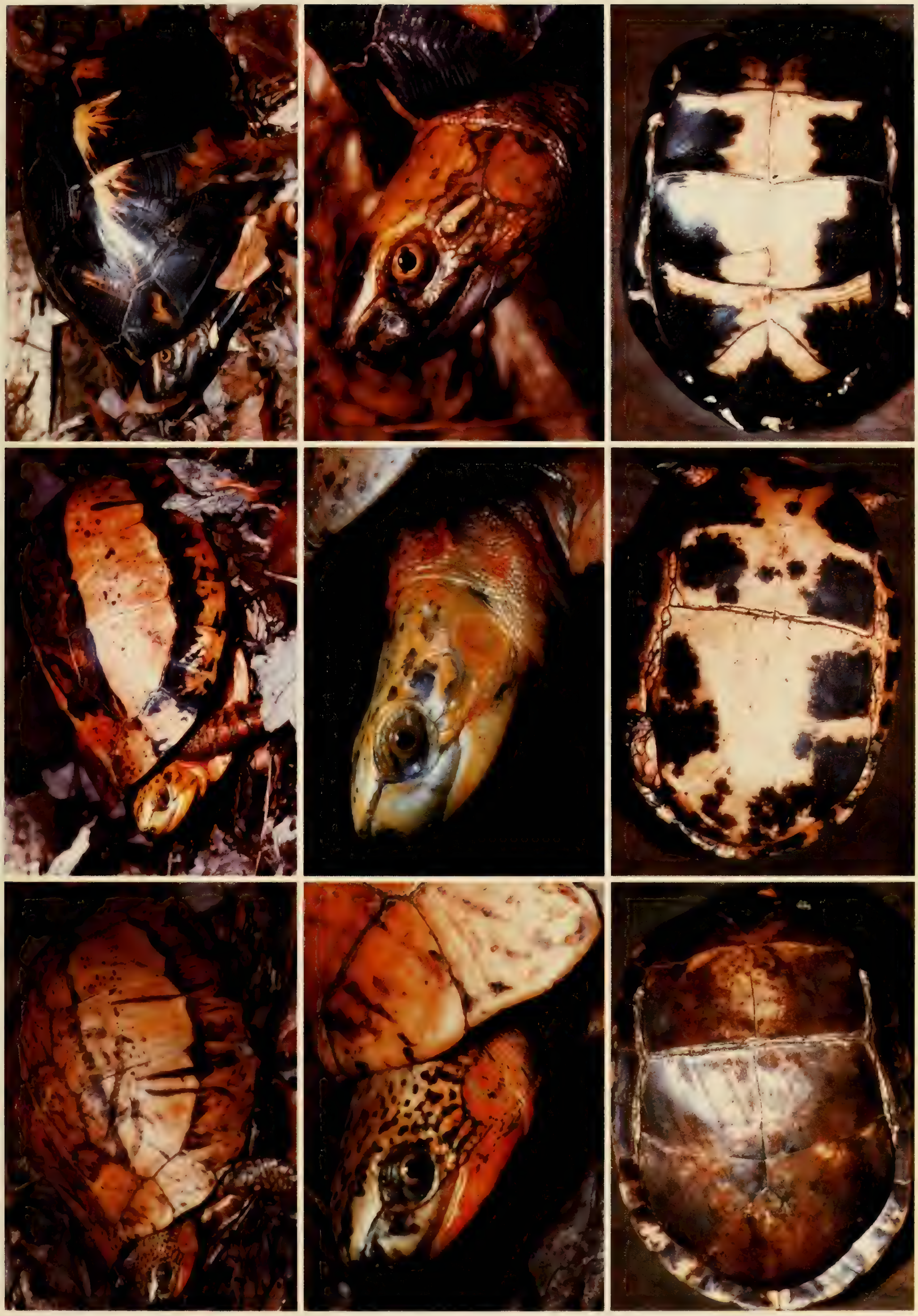
Fig. 1. Comparisons of *Cuora galbinifrons* from Vietnam (left; UF 81774), western coastal Hainan Island (center; UF 81781), and central Hainan Island (right; UF 81792).



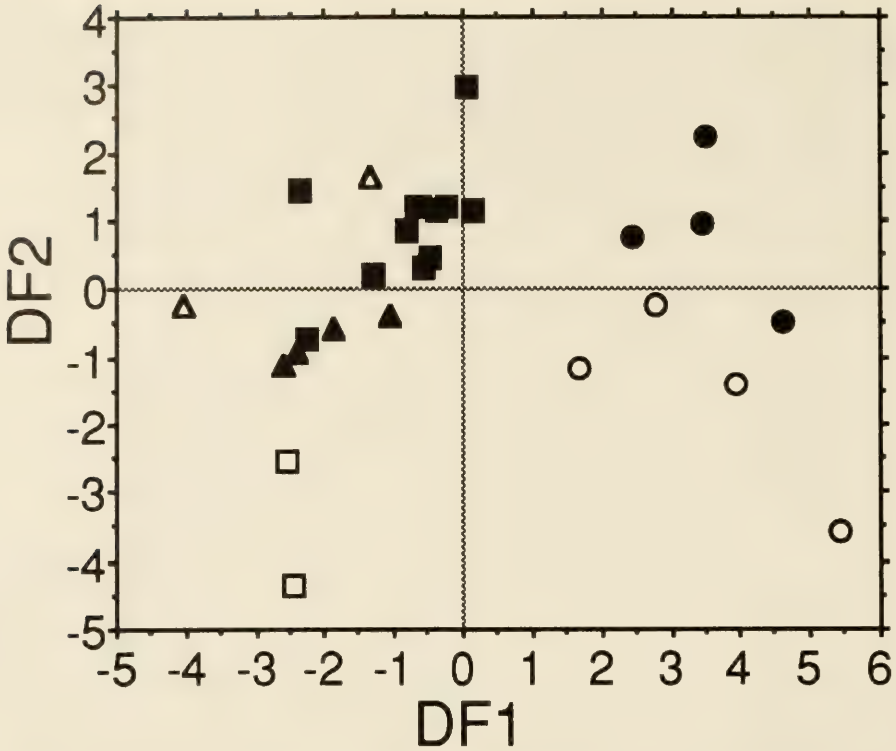


Fig. 2. Discriminant function plot of populations and sexes of *Cuora galbinifrons* from Vietnam (squares), western coastal Hainan Island (triangles), and central Hainan Island (dots) based on 12 morphometric characters (as in McCord and Iverson 1991, except not bridge length). First axis accounts for 58.3% of variation; second, 20.1%. Open symbols are males and solid symbols are females.

black with yellow streaks to mostly yellow brown with small anteriolateral black blotches.

Maximum plastron length (PL) approximately equal to carapace length (PL/CL = 0.96–1.03; mean = 1.00). Plastron slightly upturned anteriorly, with obvious hinge present between pectoral and abdominal scutes. Plastral forelobe width (PW1) at level of junction of humeropectoral seam and lateral plastral margin 48 to 51% (mean = 49%) of maximum plastron length (PL). Anterior width of plastral hindlobe (PW3: at lateral junction of abdominofemoral seam) 56 to 59% (mean = 58%) of maximum plastron length. Plastral hindlobe (HL) without an anal notch (medial length of HL 56 to 59% of maximum plastron length; mean = 57%). Bridge moderately long (bridge length/PL = 0.31 to 0.36, mean = 0.34); no axillary scute present; small inguinal scute present on yearling, lost in larger specimens. Average plastral formula: interabdominal seam (IAB) > interanal seam (IAN) > interpectoral seam (IP) ≫ intergular seam (IG) ≫ interfemoral seam (IF) ≥ interhumeral seam (IH). Interhumeral seam length/interpectoral length = 0.31 to 0.53 (mean = 0.42); interfemoral seam length/interanal length = 0.27 to 0.61 (mean = 0.39). A black blotch covering 20 to 50% of each plastral scute in adults, primarily on the older portion of the scute; blotches less extensive in subadults.

Head of medium width; upper jaw unhooked; triturating surfaces of medium width, without ridges. Small scales (not tubercles) evident between angle of jaw and tympanum. Dorsum uniform dark yellow with black flecks posteriorly. Side of head yellow to yellow orange, mottled with black. Black- or dark brown-bordered elongated (usually tear-drop shaped) yellow blotch present between orbit and tympanum. Tympanum with much less dark pigment than rest of side of head. Chin yellow, usually heavily mottled with black. Tomia dark, usually all black or heavily flecked with black.

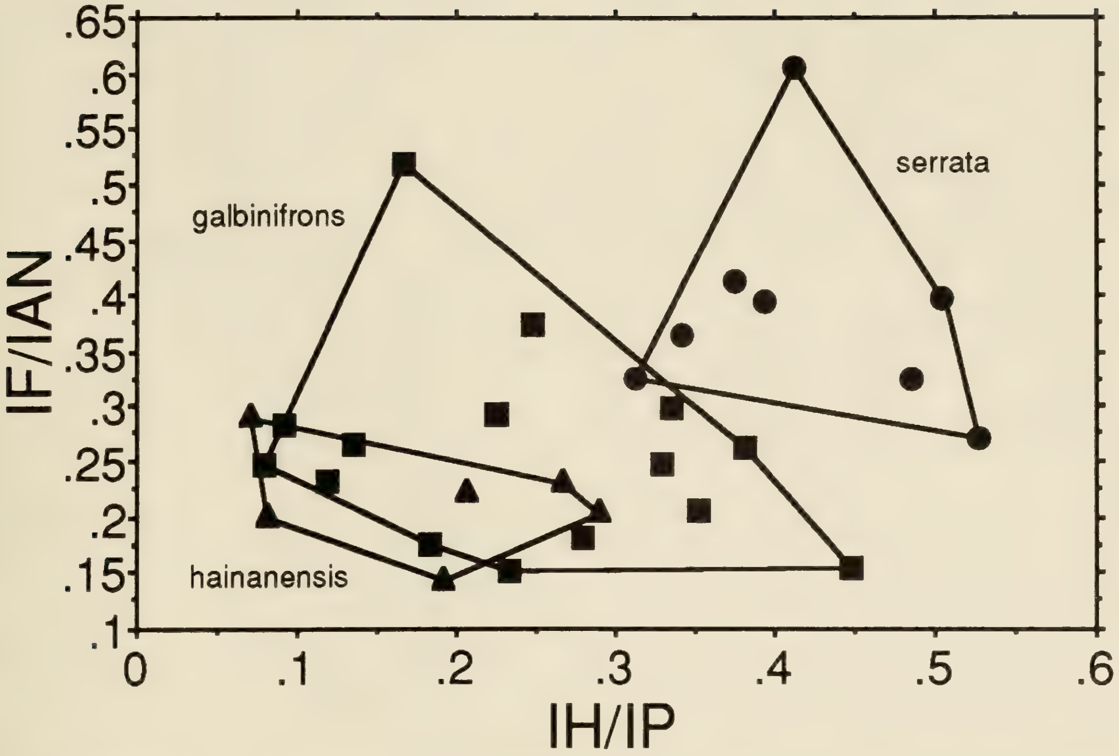


Fig. 3. Bivariate plot of the relationships among populations (sexes combined) of *Cuora galbinifrons* based on the characters IH/IP (interhumeral seam length/interpectoral length) and IF/IAN (interfemoral seam length/interanal length). Squares are *Cuora g. galbinifrons* (North Vietnam); triangles are *Cuora g. hainanensis* (western coastal Hainan Island); circles are *Cuora g. serrata* (central Hainan Island). Polygons connect most dispersed individuals of each taxon.

Antebrachium covered with large, imbricate scales, none particularly sickle-shaped; largest scales on hindlimb at heel, but much smaller than largest forelimb scales. Upper parts of limbs and tail covered with scales of medium size. Tail not particularly long, though slightly longer in males than females; base of tail thicker in males than females.

Distribution.—Known only from the type locality.

Natural history.—The medial length of the single distinct abdominal scute annulus of the smallest paratype (CL = 66 mm; PL = 61.5 mm), suggests that hatchling size was about 51 mm PL.

Remarks.—Although no specimens of *Cuora galbinifrons* were available to us from southeastern Hainan Island, descriptions of the nine types of *hainanensis* by Li (1958), Zhao (*in* Hu et al. 1975), and Koshikawa (1982) clearly indicate that those turtles are very different from *C. g. serrata* and probably identical to those on western Hainan. Specifically, southeastern Hainan turtles have no serrated shell margin, the shortest plastral scute being the humeral (often the femoral in *C. g. serrata*), no interanal seam, very little yellow pigment on the plastron, and "chestnut brown" markings on the carapace. Each of these traits clearly distinguishes them from *C. g. serrata.* In addition, Vietnam specimens of *C. galbinifrons* typically have a shell with a beige to yellow brown background, whereas those from western Hainan typically have an orange to red or pink background (Weiss 1989; this study). Although there is some uncertainty as to the exact translation of "chestnut brown" (Koshikawa 1982), that color is certainly more red than beige or yellow. Thus, specimens from southeastern and western Hainan may be indistinguishable, but direct examination of the type material of *C. hainanensis* will be necessary to confirm this hypothesis.

The taxonomic relationship between Vietnam and non-serrate Hainan Island specimens is also unclear. Morphometrically, non-serrate western Hainan specimens tend to have a slightly longer plastral hindlobe, a slightly shorter interhumeral seam, and slightly longer interpectoral and interabdominal seams than Vietnam specimens, but only the difference in hindlobe length approaches statistical significance. The discriminant function analysis (Fig. 2) also demonstrates the morphometric similarity of the populations of non-serrated turtles. However, because of the color differences mentioned above, and until more material is available for study, we recommend recognizing the non-serrate specimens from Hainan Island as *C. g. hainanensis* and those from Vietnam as the nominate subspecies.

Specimens examined.—Cuora g. galbinifrons: North Vietnam (UF 78564–68, 78570–73, 81774–80, 81787–90; WPM 1, alive). *Cuora g. hainanensis*: China, Hainan Island, western coastal area (UF 81781–86; WPM 1, alive). *Cuora g. serrata*: China, central Hainan Island (UF 81791–98; USNM 314208).

Acknowledgments

This species would not have been collected without the efforts of Oscar Shiu of Hong Kong. K. Adler, D. Auth (UF; Florida Museum of Natural History, University of Florida), J. R. Buskirk, C. H. Ernst, E. Zhao, and G. R. Zug (USNM; U.S. National Museum) provided literature, assistance, and/or pertinent information. Support for Iverson was provided by Earlham College, the Joseph Moore Museum of Natural History, and his family.

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A NEW *LEPIDODACTYLUS* (REPTILIA: GEKKONIDAE) FROM GUADALCANAL ISLAND, SOLOMONS

Walter C. Brown, Michael McCoy, and Gordon H. Rodda

Abstract.—A new species of *Lepidodactylus* (Gekkonidae) from Guadalcanal, Solomon Islands, is described. It belongs to Group I, with undivided subdigital scansors, and is related to *L. mutahi* and *L. euaensis.*

Brown & Parker (1977) recognized 13 species of the genus *Lepidodactylus* as occurring in the island region of the Indo-Australian archipelago and the Pacific, placing them in three species groups. *Lepidodactylus lugubris,* a commensal of man, with range extending beyond the boundaries of the region, is the only species in Group III. The seven species in Group I and the five species in Group II exhibit restricted ranges, often a single or small group of islands. Since 1977, two more Group I species, *L. browni* Pernetta & Black (1983) from Papua New Guinea and *L. euaensis* Gibbons & Brown (1988) from Tonga, have been described. The species described at this time is also a Group I species, known thus far only from the type locality on Guadalcanal Island. The only other Group I species thus far recorded from the Solomons is recorded only from Bougainville Island.

A single specimen of a *Lepidodactylus,* a female, was collected by McCoy from the near top of Mt. Austen, Guadalcanal Island, Solomon Islands, in September, 1978. It was examined at the time by Brown and McCoy, and identified as related to *Lepidodactylus mutahi,* differing from that species primarily in the greater number of subdigital scansors and the yellow eye ring. That specimen was not cataloged at the time, and cannot be found. In November, 1990, a second example of this species was collected by Rodda from near the top of Mt. Austen (320 m).

Lepidodactylus flavioculari s,
new species
Fig. 1

Holotype: USNM 313865, an adult male, collected on Mt. Austen, Guadalcanal Island, Solomon Islands, by Gordon H. Rodda, 23 November, 1990.

Diagnosis.—Distinguished from other species of *Lepidodactylus* by the following combinations of characters: intermediate in size, snout–vent length 49.5 mm (in life), 47.5 mm (preserved); digits dilated; toes ¼ to ½ webbed (to base of eleventh scansor on fourth toe); 18 undivided scansors below fourth toe; 10 or 11 below first toe; 38 preanal and femoral pores in a continuous series, extending almost to distal end of thigh; 12 upper labials, tenth below eye.

Description.—An intermediate-sized *Lepidodactylus,* SVL 49.5 mm in life (47.5 mm, preserved) for the male holotype; snout tapered, length 4.9 mm (53.8% of head breadth); head length 12.6 mm; head breadth 9.1 mm (72.2% of head length and 19.2% of snout–vent length); eye diameter 4.1 mm (83.7% of snout length and 45.1% of head breadth); axilla-groin distance 21.4 mm; rostral broader than high; nostril bordered by rostral, first upper labial, supranasal, postnasal and one enlarged dorsal scale; supranasals separated by three scales; 38 rows of interorbital granules; 12 upper labials, tenth below center of eye; nine lower labials; mental triangular, bordered posteriorly by

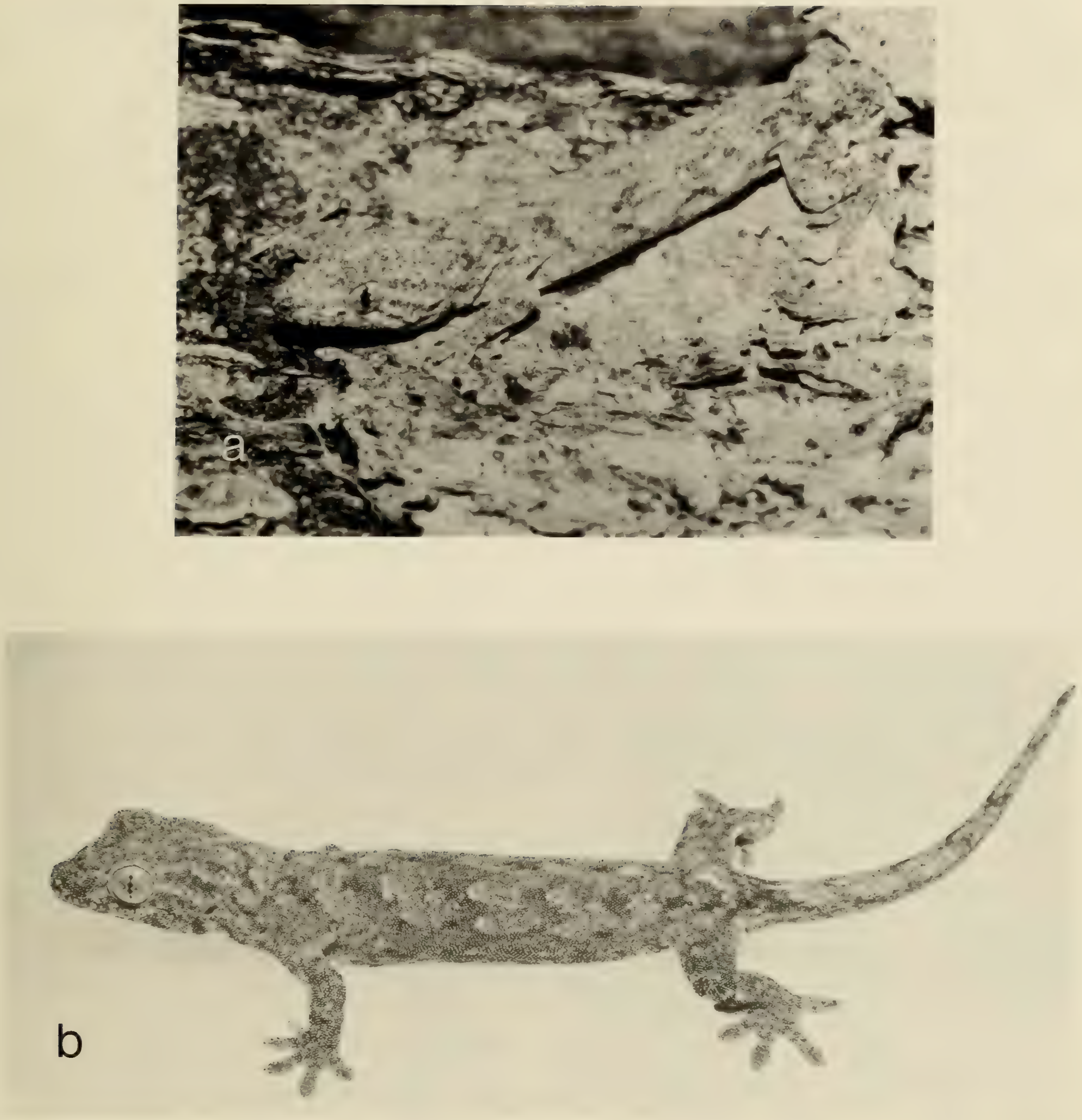

Fig. 1. a: Photograph of the holotype of *Lepidodactylus flaviocularis* (USNM 313865), a male with abbreviated tail; b: Photograph of female collected at the same locality in 1978 (specimen lost).

2(on left)–3(on right) rows of enlarged scales; dorsal and lateral surfaces covered by small, mainly uniform, granular scales; venter covered by flat scales, about 30 distinct rows at midbody, grading into granular scales on lower lateral surfaces; preanal-femoral pore scales greatly enlarged, male with 38 pores extending almost to knee, bordered anteriorly by flattened scales, as on venter, and posteriorly by small, granular scales except in region of vent; length of hind limb 15.9 mm (74.3% of axilla-groin distance); toes ¼ to ½ webbed, moderately dilated, breadth of fourth toe 26.5% of its length; scansors covering underside of toes to base, 18 under fourth toe, 10–11 under first toe; tail subcylindrical (tail of holotype broken near base and scaled-over).

Color.—Dorsal ground color, in preservative, rusty tan with some diffuse grayish

Table 1.—Snout–vent length, ratio of eye-diameter to head breadth (ED/HB), extent of webbing between third and fourth toes, and scansor and pore counts for *L. flavocularis, L. mutahi,* and *L. euaensis.* Numbers in parentheses refer to number of specimens.

Characters	*L. flaviocularis*	*L. mutahi*	*L. euansis*
SVL (mm)	47.5 (1)	37.5–56.3 (10)	41.4–50.0 (12)
Preanal and femoral pores	38 (1)	27–34 (15)	33–35 (2)
ED/HB	0.45 (1)	0.40–0.53 (14)	0.35–0.41 (8)
4th toe scansors	18 (1)	9–11 (17)	10–13 (14)
Webbing between toes 3 and 4	½ (1)	¼ (17)	⅕ (14)

blotches and small blackish flecks, most prominent on the head and neck. Lateral surfaces more gray with scattered dark flecks. Venter ivory-white with scattered dark flecks, especially under the head. Labials flecked with brown and black. In life, the venter was bright yellow on the belly region and under the hindlimbs, more creamy yellow or cream elsewhere. Eye encircled by a bright yellow ring.

Etymology.—The bright yellow eye ring is the basis for the name.

Comparison.—*Lepidodactylus flaviocularis* belongs to species Group I as defined by Brown & Parker (1977). It is most similar to *L. mutahi* from Bougainville Island of the Solomon Archipelago, and *L. euaensis* from Eua Island, Tonga (Gibbons & Brown 1988). It differs from these species primarily in the number of preanal and femoral pores, the number of scansors under the fourth toe, and the more extensive webbing between the toes (Table 1). It further differs from *L. euaensis,* as does *L. mutahi,* in the slightly larger eye relative to head breadth (Table 1). The number of scansors under the fourth toe is greater than is known for any other species in Group I. The number of preanal and femoral pores is greater than that of most species, except *L. magnus* and *L. pumilus* of New Guinea and the islands of the Torres Strait.

Habitat.—Both specimens were found near the top of Mt. Austen at 320 m elevation. The holotype was found about 3 m above the ground on 4–5 mm diameter vines suspended about 30 cm from a slender tree at the edge of a road. The primary forest at the collecting site was being altered by heavy selective logging at the time the holotype was collected. The forest was mostly intact at the time the 1978 specimen was collected.

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TWO NEW SNAPPERS (TELEOSTEI: LUTJANIDAE: APSILINAE): *PARACAESIO PARAGRAPSIMODON* ANDERSON AND KAILOLA FROM THE WESTERN PACIFIC AND *P. WALTERVADI* ANDERSON AND COLLETTE FROM THE WESTERN INDIAN OCEAN

William D. Anderson, Jr., Patricia J. Kailola, and
Bruce B. Collette

Abstract.—Two new species of *Paracaesio, P. paragrapsimodon* Anderson & Kailola (from off Ponape, Caroline Islands, and from off Port Moresby, Papua New Guinea) and *P. waltervadi* Anderson & Collette (from Walters Shoals, Madagascar Ridge, western Indian Ocean), are described from two specimens each. *Paracaesio paragrapsimodon* is easily distinguished from all other species of *Paracaesio* by the presence of prominent exserted canine teeth at anterior ends of upper and lower jaws and by its coloration in life (mostly deep metallic blue with some pale yellow on proximal halves of soft dorsal and soft anal fins, along middle of each caudal-fin lobe, and on dorsalmost parts of back and caudal peduncle), and *P. waltervadi* is recognized by the following combination of characters: tubed lateral-line scales 69 or 70, maxilla with scales, caudal-fin lunate, and coloration in life blue. A key to the species of *Paracaesio* is provided, nominal species of the *Paracaesio xanthura* complex are discussed, and brief comments on relationships of the species of *Paracaesio* are provided.

During the last several years, specimens of two previously undescribed species of the apsiline lutjanid genus *Paracaesio* have become available for study. One of these new species was collected off Ponape (now Pohnpei, according to M. Gawel, Marine Resources Division, Federated States of Micronesia, pers. comm.), Caroline Islands, and off Port Moresby, Papua New Guinea; the other, over Walters Shoals, western Indian Ocean. The goals of this paper are to describe the two new species, to compare them with other species of *Paracaesio,* to provide a key to the species of *Paracaesio,* to remark upon the nominal species of the *P. xanthura* complex, and to provide comments on the relationships of the species in the genus.

The Lutjanidae occur worldwide in warm seas. Adults of the family are largely bottom-associated, feed mainly on fishes and crustaceans, and are found from shallow inshore areas to depths of about 550 m. Some species enter estuaries and even fresh water. Early developmental stages are unknown for most species, but the early stages that have been described are pelagic. There are 17 genera and about 105 species (including the 2 described herein) of lutjanids, currently classified in 4 subfamilies—Etelinae (5 genera and 19 species), Apsilinae (4 genera and 12 or 13 species), Paradicichthyinae (2 genera and 2 species), and Lutjaninae (6 genera and 72 species). Some lutjanids reach sizes as great as 100 to 120 cm. Many are important to sport and/or commercial fishermen, and many are fine food fishes, although some are ciguatoxic in certain areas.

Institutional abbreviations follow Leviton et al. (1985); nm denotes nautical miles; SL, standard length; TL, total length; ICZN, the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1985).

Methods

Methods for making counts and measurements follow Randall et al. (1987), except as noted below. Osteological data were taken from radiographs. Gillrakers and pseudobranchial filaments were counted on the right side. The most anterior scale in dorsal midline was considered the first predorsal scale; counts of predorsal scales were made in midline, as nearly as possible, and did not include smaller scales at base of first dorsal spine. The first vertebra with a haemal spine was considered the first caudal vertebra; the urostylar vertebra, the last. Postorbital length of head was distance between posteriormost point of fleshy orbit and posteriormost point of opercular membrane. Lower jaw to branchiostegal membranes was measured from symphysis of dentaries to junction of branchiostegal membranes. Maxilla width was greatest width of posterior expansion of maxilla. Length of lower jaw was measured from anteriormost point on dentary to posteriormost point on angular. Interorbital width was least bony measurement. Internarial distance was distance between posterior border of anterior naris and anterior border of posterior naris. Posterior naris to orbit was measured from posterior border of posterior naris to anterior border of fleshy orbit. Teeth were measured from points where they emerge from jaws (as nearly as possible) to their distal tips. (The point of emergence of a tooth can be difficult to ascertain due to the large amount of fleshy tissue overlying the alveolar surfaces of the jaws.) Depth of body was taken vertically from base of first dorsal spine. Length of caudal peduncle was distance from posterior end of base of anal fin to mid-base of caudal fin. Length of anal-fin base was from anteriormost point of base of first anal spine to posteriormost point of base of last anal soft ray. Length of anal fin was from anteriormost point of base of first anal spine to distal tip of anal fin with fin depressed against body. Upper and lower lobes of caudal fin were measured from mid-base of caudal fin to distal tip of longest ray in each lobe. Most measurements are given as percentages of SL, a few as percentages of snout length and postorbital head length, and some as quotients of SL or head length rounded to the nearest 0.05.

Sketches of caudal-fin shapes (Fig. 1), except Fig. 1H, were made by photocopying the maximally spread fins of the specimens illustrated, tracing the outlines of the photocopied fins, and photoreducing the tracings to approximately the same sizes. The same procedure was used for Fig. 1H, except an illustration from Kyushin et al. (1982) was photocopied.

Apsilinae

There are no known synapomorphies distinguishing the species of Lutjanidae from those of other percoid families. Johnson (1981:1) treated the Lutjanidae as a natural group because of "the obvious intermediacy of the Apsilinae between the Etelinae and Lutjaninae." Although we are not aware of any synapomorphies for the Apsilinae, the following combination of traits characterizes the subfamily. Nares on each side close together; posterior flap of anterior nostril when reflected typically reaching anterior border of posterior nostril. Vomerine teeth present. Dorsal and anal fins naked. Dorsal-fin rays X, 10 (rarely X, 9). Anal-fin rays III, 8 (occasionally III, 9). Anterior dorsal and anterior anal soft rays not produced into filaments. Ultimate soft ray of dorsal fin and anal fin not produced or produced only slightly, usually shorter than penultimate soft ray. Caudal fin emarginate to deeply forked. Procurrent caudal-fin rays 11 to 13 dorsally, 10 to 13 ventrally. Interorbital region transversely somewhat flattened to strongly convex. Posteriormost 4–8 complete pterygiophores of dorsal fin and posteriormost 5–7 complete pterygiophores of anal fin trisegmental. Adductor mandibulae without division A_1'. For more detailed descriptions of the Lutjanidae and Apsilinae, see Johnson (1981) or Anderson (1987). The genera of Apsilinae are: *Apsilus* (2 species), *Lipocheilus* (1 species), *Parapristipomoides* (1 species), and *Paracaesio* (about 8 or 9 species).

Paracaesio Bleeker, 1875

Paracaesio Bleeker, 1875:38 (type species *Caesio xanthura* Bleeker, 1869, by monotypy).

Vegetichthys Tanaka, 1917:7 (type species *Vegetichthys tumidus* Tanaka, 1917 [=*Caesio xanthura* Bleeker, 1869], by monotypy).

Aetiasis Barnard, 1937:59 (type species *Aetiasis cantharoides* Barnard, 1937 [apparently = *Caesio xanthura* Bleeker, 1869], by monotypy).

Diagnosis.—A genus of apsiline lutjanid fishes characterized by the following: interorbital region transversely strongly convex; anterior end of upper lip without a thick fleshy protrusion; gillrakers 7 to 12 + 16 to 24—total 26 to 35; adductor mandibulae section A_1 without an anterodorsal extension; ultimate dorsal soft ray 50 to 90% length of penultimate; ultimate anal soft ray 65 to 95% length of penultimate; pectoral fin about 90 to 125% of head length (in specimens more than about 150 mm SL, almost always 102 to 125% of head length).

Gender.—Most authors have treated *Paracaesio* as if it were a masculine noun, but George C. Steyskal has advised that it is feminine. Consequently, adjectival specific names for species of *Paracaesio* that have been spelled with the *-us* termination must be emended to end in *-a* (ICZN, Article 31b). (See Carpenter 1987:5 for a discussion of the gender of *Paracaesio*.)

Species of Paracaesio.—Anderson (1987) recognized six species of *Paracaesio*; recent work indicates that there are about eight or nine species. Based on numbers of tubed scales in the lateral line, the genus appears to be made up of two natural groups of species—one with from 47 to 50 scales in the lateral line, the other with from 68 to 73. Within a species group the best characters for identification are maxillary squamation (presence or absence), coloration, and shape of the caudal fin. Museum specimens can be very difficult to identify because coloration is usually lost and the caudal fins are often damaged. *Paracaesio* ranges widely through the Indo-Pacific.

Key to Species of *Paracaesio*

1a. Tubed lateral-line scales 68–73. Caudal fin forked or lunate (Fig. 1A–F) 2
1b. Tubed lateral-line scales 47–50. Caudal fin lunate or emarginate (Fig. 1G–J) 5
2a. Several prominent exserted canine teeth at anterior ends of upper and lower jaws (longest anterior tooth in upper jaw 6.3–8.7% postorbital head length, longest anterior tooth in lower jaw 6.5–6.9% postorbital head length; Fig. 2A). Maxilla without scales .... *P. paragrapsimodon,* n. sp.
2b. Teeth at anterior ends of jaws smaller, rarely prominent (longest anterior tooth in upper jaw 2.4–5.9% postorbital head length, $\bar{X} = 3.96$; longest anterior tooth in lower jaw 1.3–6.0% postorbital head length, $\bar{X} = 3.08$; Fig. 2B, C). Maxilla with or without scales 3
3a. Caudal fin lunate (Fig. 1F). Coloration in life blue, without any yellow. Maxilla with scales .... *P. waltervadi,* n. sp.
3b. Caudal fin forked (Fig. 1B–E). In life caudal fin and much of upper body yellow or if yellow absent,

general body color dark violet. Maxilla with or without scales .. 4

4a. General body color dark violet; fins reddish brown. Preopercle with one to three rows of scales peripheral to and usually distinctly separated from main group of cheek scales. Maxilla without scales .... *P. sordida* Abe & Shinohara, 1962; Indo-west Pacific

4b. Caudal fin, upper part of caudal peduncle, and upper side of body to anterior end of dorsal fin yellow; remainder of body mostly blue. Preopercle without rows of scales peripheral to main group of cheek scales. Maxilla with or without scales ....*P. xanthura* complex

5a. Maxilla with scales. Caudal fin lunate (middle of distal margin of caudal fin of *P. kusakarii* becoming rounded with age, Fig. 1G, H) ... 6

5b. Maxilla without scales. Caudal fin lunate or emarginate (Fig. 1I, J) .. 7

6a. Yellow band running from anterior end of lateral line obliquely to about middle of dorsal fin. Eight broad dark vertical bars in life (still recognizable on holotype when examined in Dec 1982, several years after preservation). Nape without pronounced hump. Middle of distal margin of caudal fin not rounded with age .... *P. gonzalesi* Fourmanoir & Rivaton, 1979; western Pacific[1]

6b. No oblique yellow band on side of body. Four broad dark vertical bars on upper side of body. Large individuals with pronounced hump on nape as a result of higher supraoccipital crest. Middle of distal margin of caudal fin becoming rounded with age (Fig. 1G, H) (Senta in Kyushin et al. 1982:68) .... *P. kusakarii* Abe, 1960; central and western Pacific

7a. General color cerulean blue, without vertical bars. Caudal fin lunate (Fig. 1I) .... *P. caerulea* (Katayama, 1934); western Pacific

7b. General color light brown dorsally and silver ventrally with four or five broad brown to dark gray vertical bars on body extending from dorsal surface to midline or below midline laterally. Caudal fin emarginate (Fig. 1J) .... *P. stonei* Raj & Seeto, 1983; central and western Pacific

Paracaesio paragrapsimodon Anderson & Kailola, new species, and *P. waltervadi* Anderson & Collette, new species

Because *Paracaesio paragrapsimodon* and *P. waltervadi* are identical in many traits, it is appropriate, in order to avoid repetition, to characterize these two species under a single heading and then to elaborate as necessary under the respective species accounts. The observations presented herein apply to the four type specimens of these two new species.

Dorsal-fin rays X, 10. Anal-fin rays III, 8. Pectoral-fin rays 17. Pelvic-fin rays I, 5. Principal caudal-fin rays 9 + 8; branched rays 8 + 7. Branchiostegal rays 7. Cheek scale rows 7. Vertebrae 24 (10 precaudal + 14 caudal). Formula for predorsal (=supraneural) bones, anterior neural spines, and anterior dorsal pterygiophores 0/0/0 + 2/1 + 1/1/ (using symbolization of Ahlstrom et al. 1976). Pleural ribs on vertebrae 3 through 10. Parhypural and five hypurals present; hypurals: 1 & 2 fused, 3 & 4 fused, 5 autogenous. Epurals 3.

Mouth terminal. Premaxillae protrusile.

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[1] Raj & Seeto (1983) reported that *P. gonzalesi* has a naked maxilla, but the first author examined the holotype of this species and found scales on the maxillae. Maxillary squamation may be a labile character in *P. gonzalesi*, as it is in the *P. xanthura* complex.

Maxilla reaching posteriorly to a vertical well past anterior border of eye. No supramaxilla. Preopercle without spine at angle. Free margin of interopercle smooth. Dorsal fin single, not incised between spinous and soft portions. Ventral (trailing) edge of anal fin almost parallel to ventral body contour. Pectoral fin asymmetrical, longest rays in dorsal part of fin. Lateral line complete, running parallel to dorsal body contour below dorsal fin and near mid-lateral axis of body on caudal peduncle. Scales finely ctenoid, with rows of ctenial bases (Hughes 1981) present proximal to marginal cteni. No secondary squamation. Cheek, interopercle, subopercle, opercle, and temporal region scaly; predorsal scales extending anteriorly to about level of middle of eye; fairly wide naked band ventral and posterior to orbit, this band continuous with naked lachrymal region anteriorly and naked part of interorbital region posterodorsally; naked band running obliquely from interorbital region anteriorly to scale bone (superficial projection of posttemporal bone) posteriorly—this naked band separating temporal scales from predorsal scales; temporal scales usually in two groups separated by a scaleless area—anteroventral group composed of small scales, posterodorsal group of large scales (of about same size as other head scales); remainder of head without scales (except maxilla scaly in *P. waltervadi*). Dorsal and anal fins without scales; other fins scaly basally; pelvic axillary and interpelvic processes well developed.

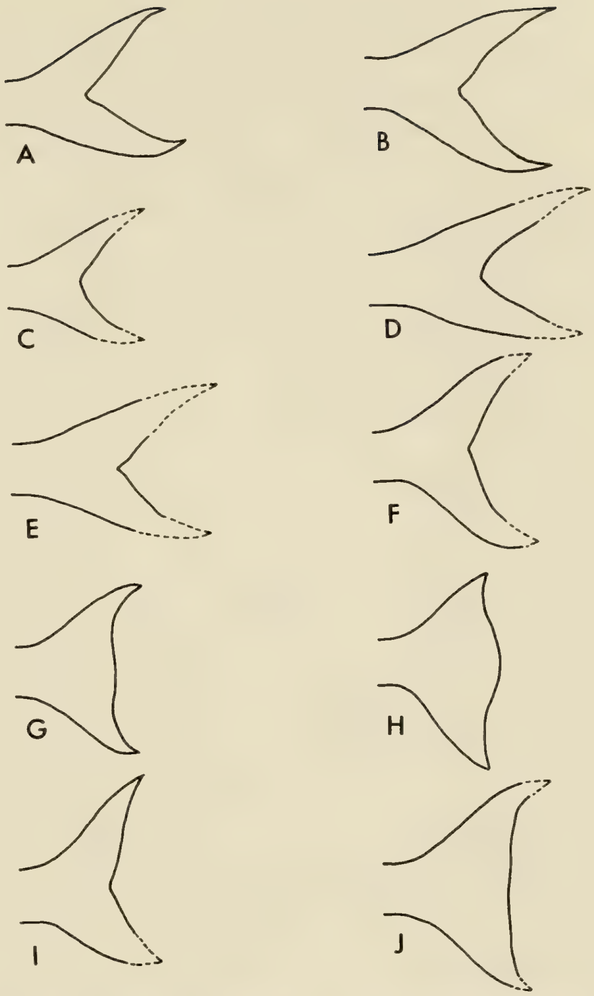

Fig. 1. Caudal-fin shapes in species of *Paracaesio*. A, Paratype of *P. paragrapsimodon*, AMS I. 31427-001, 197 mm SL; Basilisk Passage, off Port Moresby, Papua New Guinea. B, *P. sordida*, BPBM 11143, 269 mm SL; Ua Pou, Marquesas Islands. C, Putative syntype of *Caesio xanthura* (=*P. xanthura*), RMNH 3948, 128 mm SL; off Madagascar. D, Holotype of *P. pedleyi* (may = *P. xanthura*), AMS I. 13885, 306 mm SL; off Lord Howe Island. E, Putative holotype of *Aetiasis cantharoides* (apparently = *P. xanthura*), SAM 18430, 355 mm SL; off Durban, Natal, Republic of South Africa. F, Holotype of *P. waltervadi*, USNM 307769, 412 mm SL; Walters Shoals, Madagascar Ridge. G, *P. kusakarii*, GMBL 76-436, 353 mm SL; Dumbéa Pass, New Caledonia. H, *P. kusakarii* (redrawn from Kyushin et al. 1982), 544 mm SL. I, *P. caerulea*, BPBM 19170, 315 mm SL; fish market, Naha, Okinawa. J, *P. stonei*, GMBL 81-65, ca. 400 mm SL; off Masefau, Tutuila Island, American Samoa. (Broken lines indicate reconstructions of broken caudal-fin lobes.)

Paracaesio paragrapsimodon
Anderson & Kailola, new species
Figs. 1A, 2A, 3; Table 1

Holotype.—USNM 269287, 275 mm SL, male; Ponape, Caroline Islands; R. Croft; 1984.

Paratype.—AMS I.31427-001, 197 mm SL, male; Basilisk Passage, off Port Moresby, Papua New Guinea; 200 m; L. Aitsi; Feb 1988; handline.

Diagnosis.—A species of *Paracaesio* distinguished by the presence of several prominent exserted canine teeth at anterior ends of upper and lower jaws (compare Fig. 2A,

Table 1.—Data on morphometric characters for *Paracaesio paragrapsimodon* and *P. waltervadi.* Standard lengths are in mm; other measurements, in percentages of standard length; > = slightly damaged, bk. = broken.

	P. paragrapsimodon		*P. waltervadi*	
Character	Holotype USNM 269287	Paratype AMS I. 31427-001	Holotype USNM 307769	Paratype IOAN uncat.
Standard length	275	197	412	429
Head, length	28.7	30.2	27.0	27.5
Snout, length	9.1	8.5	8.3	9.0
Orbit, diameter	8.0	10.2	6.8	6.6
Postorbital length of head	12.1	13.2	12.1	12.8
Lower jaw to branchiostegal membranes	10.2	12.2	10.0	9.8
Upper jaw, length	11.2	11.5	10.0	10.7
Maxilla, width	3.3	4.1	3.0	3.0
Lower jaw, length	13.3	14.2	11.7	12.2
Interorbital width	9.1	9.6	9.3	10.5
Suborbital depth	1.9	1.9	1.8	2.0
Internarial distance	0.36	0.33	0.44	0.29
Posterior naris to orbit	2.7	2.6	2.7	2.9
Longest tooth, upper jaw	1.05	0.84	ca. 0.36	0.30
Longest tooth, lower jaw	0.84	0.86	ca. 0.39	0.33
Body, depth	32.9	34.9	34.9	34.4
Predorsal length	37.2	37.6	36.3	36.5
Preanal length	60.4	62.3	65.8	62.2
Caudal peduncle, length	18.7	21.9	22.0	21.0
Caudal peduncle, depth	8.1	9.0	9.0	9.8
Pectoral fin, length	>31.9	35.6	28.4	25.5
Pelvic fin, length	20.1	20.8	18.9	18.9
Anal fin base, length	19.8	21.0	18.6	21.4
Anal fin, length	29.7	33.4	>28.5	>30.5
Upper caudal-fin lobe, length	30.5	32.9	>30.8	bk.
Lower caudal-fin lobe, length	29.5	32.9	>27.8	bk.
Caudal concavity	ca. 16.7	20.0	ca. 13.7	—
First dorsal spine, length	ca. 5.9	>5.7	6.3	6.9
Third dorsal spine, length	bk.	14.7	11.3	>11.6
Longest dorsal spine, length	bk.	>15.5 (4th)	12.3 (4th)	bk.
Penultimate dorsal soft ray	>12.4	17.0	>11.3	bk.
Ultimate dorsal soft ray	>8.8	10.8	10.1	bk.
First anal spine, length	>3.5	5.0	4.3	>3.6
Second anal spine, length	>7.1	9.0	6.0	>6.8
Third anal spine, length	bk.	9.8	>6.8	>7.7
Penultimate anal soft ray	ca. 11.1	15.0	>11.4	>11.6
Ultimate anal soft ray	8.2	9.6	>10.4	9.7

B, & C; longest tooth in upper jaw 9.9–11.6% snout length, 6.3–8.7% postorbital head length; longest tooth in lower jaw 9.2–10.2% snout length, 6.5–6.9% postorbital head length); tubed scales in lateral line 69 or 70; maxilla without scales; caudal fin deeply forked.

Description.—Characters included in the combined description of *P. paragrapsimodon* and *P. waltervadi* and those in the species diagnosis are part of the species description. Data for the paratype are presented in parentheses where they differ from those for the holotype. Depth of body 3.05 (2.85), length of head 3.50 (3.30) in SL. Length of snout 3.15 (3.55), orbital diameter 3.60 (2.95), interorbital width 3.15 in length of head. Additional morphometric data appear in Table 1. Procurrent caudal-fin rays 13 (12) dorsally, 12 ventrally. Pseudobranchial filaments ca. 46 (ca. 37). Gillrakers 9 + 20 (21)—total 29 (30), no rudiments present. Tubed lateral-line scales 69 left, 70 right. Predorsal scales ca. 22 (21). Scale rows between middle of spinous dorsal fin and lateral line 7 (8). Scales between origin of dorsal fin and lateral line 9 (ca. 9). Scales between origin of anal fin and lateral line 18 (19). Circum-caudal-peduncle scales 28 (ca. 28). Posteriormost 8 (7) complete pterygiophores of dorsal fin and posteriormost 6 of anal fin trisegmental. Epipleural ribs associated with first 8 (9) vertebrae.

Flap on posterior border of anterior naris falling slightly short of posterior naris when reflected. Anteriormost part of fleshy orbit of holotype with numerous short papillae. Both free margins of preopercle almost smooth except for small serrae in region of angle. Free margin of subopercle smooth. Longest gillrakers longer than longest gill filaments. Two dorsalmost and two ventralmost pectoral-fin rays unbranched, other rays branched; pectoral fin reaching to about a vertical through base of second dorsal soft ray (vertical between bases of fourth and fifth dorsal soft rays) and reaching vertical through base of third anal spine (vertical through base of first anal soft ray). Pelvic fin inserted a little posterior to base of pectoral fin, tip reaching vertical through base of tenth dorsal spine, falling well short of anal fin. Caudal fin deeply forked. Anteroventral group of temporal scales composed of one or two rows of small scales, posterodorsal group of three or four rows of large scales.

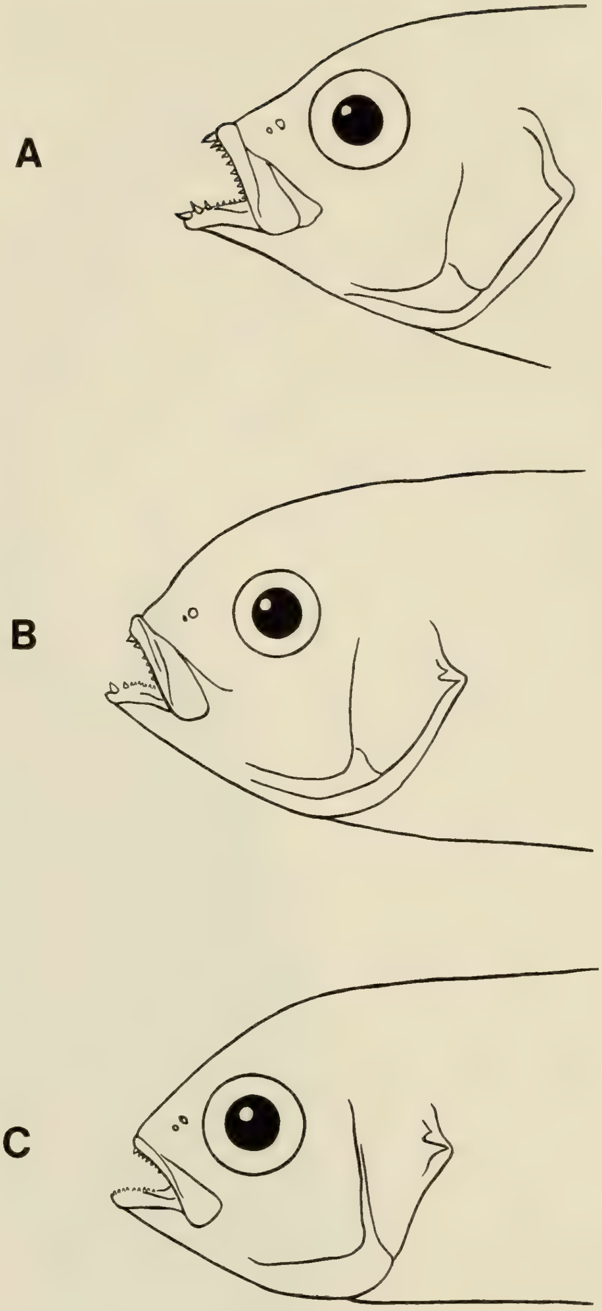

Fig. 2. Anterior jaw dentition in three nominal species of *Paracaesio*. A, Holotype of *P. paragrapsimodon*, USNM 269287, 275 mm SL; Ponape, Caroline Islands. B, Holotype of *P. pedleyi* (may = *P. xanthura*), AMS I. 13885, 306 mm SL; off Lord Howe Island. C, Putative syntype of *Caesio xanthura* (=*P. xanthura*), RMNH 3948, 128 mm SL; off Madagascar.

Dentition.—Holotype: Premaxilla with outer row of caniniform teeth; two very well-developed exserted canines on each side near symphysial diastema; a single caniniform tooth on each side of and immediately adjacent to diastema—these two teeth slightly posterior to most anterior canines; medially a band of very small teeth paralleling outer row of teeth, this band expanded anteriorly into a triangular patch in area adjacent to symphysis. Dentary with outer row of conical teeth along side of jaw; paralleling this row medially a band of smaller conical teeth—band expanded adjacent to sym-

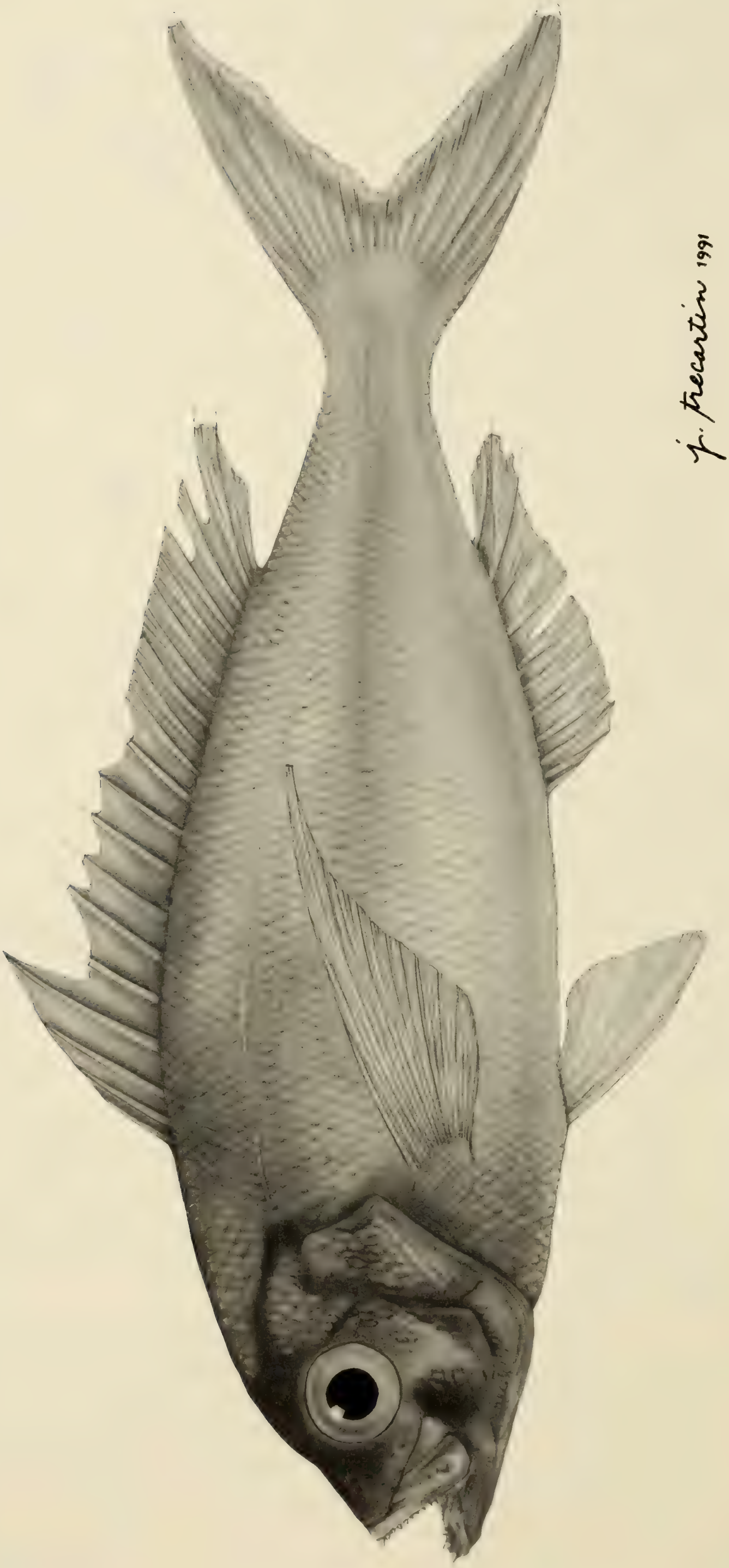

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Fig. 3. Holotype of *Paracaesio paragrapsimodon,* USNM 269287, 275 mm SL; Ponape, Caroline Islands.

physial diastema; four very well-developed, strongly exserted canines on left (three on right) at anterior end of jaw; on right a smaller canine close to posterolateral base of exserted canine nearest symphysis. Vomerine teeth small—in roughly triangular patch, with apex of patch directed anteriorly. Palatine with narrow band of small teeth. No teeth on tongue or pterygoids.

Paratype: Dentition similar to that of holotype except teeth in inner band on premaxilla relatively larger than in holotype and band not as expanded anteriorly as in holotype; on dentary inner band of teeth developed only at anterior end of jaw.

Live coloration.—No information available on live coloration of holotype. When freshly caught, body of paratype was deep metallic blue; proximal halves of soft dorsal and soft anal fins pale yellow, with yellow extending onto dorsalmost part of back and dorsal part of caudal peduncle; yellow along middle of each caudal-fin lobe and at posterior margin of caudal fin.

Coloration in alcohol.—Holotype: General body color gray; dorsum of head much darker; evidence of what may have been vertical bars on sides of body; dorsal-fin membrane dusky; pectoral, pelvic, and anal fins mostly hyaline; caudal-fin membrane for most part straw colored to dusky, hyaline distally.

Paratype: Body slate blue dorsally and laterally, grayish ventrally; scaleless part of dorsum of head purplish blue, scaly part darker; sides of head bluish gray to gray, lighter ventrally; fins similar to those of holotype.

Comparisons.—*Paracaesio paragrapsimodon* is readily distinguished from all other species of *Paracaesio* by the possession of prominent exserted canine teeth at anterior ends of upper and lower jaws and by the pattern of coloration; from *P. caerulea, P. gonzalesi, P. kusakarii,* and *P. stonei* by its high count of lateral-line scales (69 or 70 vs. 47–50); from *P. gonzalesi, P. kusakarii,* and *P. waltervadi* by absence of scales on the maxilla; from *P. sordida* by absence of preopercular scales peripheral to main group of cheek scales; and from all species except *P. sordida* and those of the *P. xanthura* complex by shape of the caudal fin (Fig. 1).

Distribution.—Known only from the type specimens, one collected in the western Pacific Ocean off Ponape, Caroline Islands, and the other in Basilisk Passage, off Port Moresby, Papua New Guinea. Depth of capture, 200 m, is known only for the specimen from Basilisk Passage.

Etymology.—The name *paragrapsimodon* is from the Greek—paragrapsimos (exceptional), odon (tooth)—referring to the prominent exserted canine teeth at anterior ends of upper and lower jaws of this new species. The name of this new species is a noun in apposition to the generic name *Paracaesio.*

Paracaesio waltervadi

Anderson & Collette, new species

Figs. 1F, 4; Table 1

Paracaesio sp., Collette & Parin, 1991:11, pl. If (brief description and color illustration; two specimens collected at Walters Shoals during R/V *Vityaz* cruise 17).

Holotype.—USNM 307769, 412 mm SL, male; Walters Shoals, Madagascar Ridge, western Indian Ocean; 33°12′S, 43°52′E; 18–40 m; R/V *Vityaz* cruise 17, station 2751; 22 Dec 1988; handline.

Paratype.—IOAN uncat., 429 mm SL, male; Walters Shoals, Madagascar Ridge, western Indian Ocean; 33°16′S, 43°53′E, 35–40 m; R/V *Vityaz* cruise 17, station 2683a; 11 Dec 1988; handline.

Diagnosis.—A species of *Paracaesio* distinguished by the following combination of characters: tubed scales in lateral line 69 or 70; maxilla with scales; caudal fin lunate; coloration in life blue; jaws without prominent exserted teeth anteriorly (longest tooth in upper jaw 3.4–ca. 4.4% snout length, 2.4–ca. 3.0% postorbital head length; longest

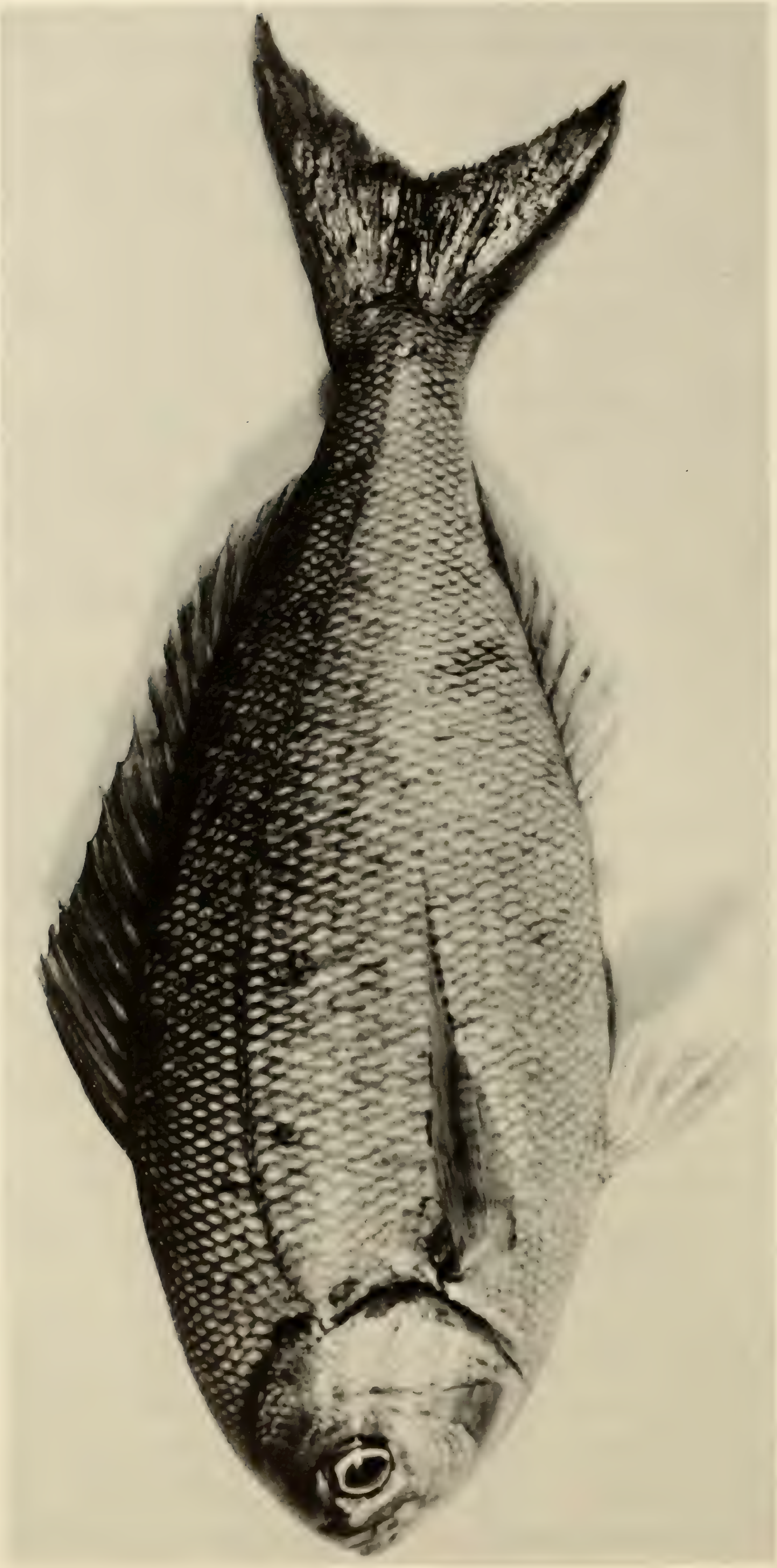

Fig. 4. Paratype of *Paracaesio waltervadi*, IOAN uncat., 429 mm SL; Walters Shoals, Madagascar Ridge.

tooth in lower jaw 3.6–ca. 4.7% snout length, 2.5–ca. 3.2% postorbital head length).

Description.—Characters included in the combined description of *P. paragrapsimodon* and *P. waltervadi* and those in the species diagnosis form part of this description. Data for the paratype are presented in parentheses where they differ from those for the holotype. Depth of body 2.85 (2.90), length of head 3.70 (3.65) in SL. Length of snout 3.25 (3.05), orbital diameter 3.95 (4.20), interorbital width 2.90 (2.60) in length of head. Additional morphometric data appear in Table 1. Procurrent caudal-fin rays 12 (ca. 12) dorsally, 12 (ca. 11) ventrally. Pseudobranchial filaments ca. 56, difficult to count (not counted on paratype). Gillrakers 11 (8) + 22 (21)—total 33 (29), no rudiments present. Tubed lateral-line scales 70 both sides (70 left, 69 right). Predorsal scales ca. 22. Scale rows between middle of spinous dorsal fin and lateral line 7½ (7). Scales between origin of dorsal fin and lateral line 10 (9). Scales between origin of anal fin and lateral line 18. Circum-caudal-peduncle scales 29 (28). Posteriormost 7 complete pterygiophores of dorsal fin and posteriormost 6 of anal fin trisegmental. Epipleural ribs associated with first 8 vertebrae.

Anterior naris with poorly developed flap on posterior border, flap falling well short of (almost reaching on right side of paratype) posterior naris when reflected. Both free margins of preopercle essentially smooth (scalloped in region of angle on paratype). Free margin of subopercle with a few serrae near junction with interopercle on right side, smooth on left (smooth on both sides of paratype). Longest gillrakers shorter than longest gill filaments. Two dorsalmost and ventralmost pectoral-fin rays unbranched, other rays branched; pectoral fin reaching vertical between bases of first and second dorsal soft rays and about reaching vertical through posterior border of vent. Pelvic fin inserted well posterior to vertical through base of pectoral fin; tip about reaching vertical through base of ninth dorsal spine, falling well short of vent. Caudal fin lunate. Anteroventral group of temporal scales in curving row on left, in about three rows of unequal length on right (anteroventral group absent on right of paratype); posterodorsal group of temporal scales in about five rows; space between groups of temporal scales narrowly bridged (not bridged on paratype) by row of scales on left—this row continuous with anteroventral row of scales.

Premaxilla with outer row of conical teeth, anteriorly a few of these teeth enlarged into caniniform teeth; medially a band of very small teeth, band somewhat expanded anteriorly adjacent to symphysial diastema. Dentary with outer row of small conical teeth; medially a band of very small teeth, band expanded anteriorly adjacent to symphysial diastema; at anterior end of jaw several widely spaced caniniform teeth—these teeth jutting somewhat obliquely from jaw. Vomer and palatine with very fine teeth; vomerine teeth apparently in triangular patch, with apex directed anteriorly; palatine teeth in narrow band. No teeth on tongue or pterygoids. (Teeth are especially difficult to examine because most are quite small, alveolar surfaces of jaws are very fleshy, and jaws are difficult to open widely enough to allow easy examination of dentition. Teeth of paratype not examined in detail because jaws are tightly closed.)

Collette & Parin (1991:7, pl. If) published a color photograph of the paratype taken shortly after capture. A color photograph of the holotype shows head and dorsal part of body to be blue, body lighter blue ventrally; dorsal, pectoral, and caudal fins and posterior three-fourths of anal fin blue; anterior part of anal fin and pelvic fin hyaline. In alcohol, body and head slate blue dorsally (except scaleless part of dorsum of head bluer), paler ventrally; dorsal fin and most of caudal fin slate blue; outermost rays of both lobes of caudal fin straw colored, distal margin of caudal fin pale gray to hyaline; other fins grayish to hyaline.

Comparisons.—*Paracaesio waltervadi* is distinguished from all other species of the genus by its coloration in life (blue without any yellow); from *P. caerulea, P. gonzalesi, P. kusakarii,* and *P. stonei* by its high count of lateral-line scales (69 or 70 vs. 47–50); from *P. paragrapsimodon, P. sordida, P. caerulea,* and *P. stonei* by presence of scales on the maxilla; from *P. sordida* by absence of preopercular scales peripheral to main group of cheek scales; and from *P. paragrapsimodon, P. sordida,* the *P. xanthura* complex, and *P. stonei* by shape of the caudal fin.

Distribution.—Known only from the type specimens collected in the western Indian Ocean over Walters Shoals in depths ranging from 18 to 40 m. Walters Shoals, an isolated seamount (33°9–16′S, 43°49–56′E), reaching to within 18 m of the surface, is located about 400 nm south of Madagascar and 600 nm east of South Africa (Collette & Parin 1991).

Etymology.—The name *waltervadi* is derived from Walters and vadum, Latin for shoal.

Species of the *Paracaesio xanthura* Complex

We include four nominal species here; three of them (*Paracaesio pedleyi, P. tumida,* and *P. cantharoides*) were considered by Allen (1985) and Anderson (1987) as junior synonyms of the fourth, *P. xanthura.* As a result of new information, in part derived from examination of additional material, a reassessment of all four species is in order.

Paracaesio xanthura.—The first author has examined the putative syntypes (RMNH 3948, 128 mm SL, and RMNH 5716, 196 mm SL) of *Caesio xanthura* Bleeker, 1869 (=*Paracaesio xanthura*) and 18 other specimens (55–355 mm SL) that he identified as this species. The type locality for *P. xanthura* is off the island of Nossi-Bé (just off the northwest coast of Madagascar in the Mozambique Channel), and the range of the species is generally considered to include much of the Indo-Pacific.

There are inconsistencies in literature descriptions of live coloration and maxillary squamation of *P. xanthura.* In Bleeker's (1869) original description of *Caesio xanthura,* the coloration is given, in part, as—anterodorsal part of body cerulean, posteroventrally a beautiful yellow; caudal yellow dorsally and ventrally, somewhat dark margined. Illustrations in Masuda et al. (1984, pl. 154H) and Allen (1985, pl. XXIV, fig. 89) show a broad yellow band on upper side of body beginning at about anterior end of dorsal fin, continuing over most of caudal peduncle, and extending posteriorly out onto both lobes of caudal fin. Yoshino (in Masuda et al. 1984:168) reported that the maxilla of *P. xanthura* lacks scales, but Allen (1985) and Anderson (1987) stated that scales may be present or absent on the maxilla. Anderson's (1987) statement was based on his examination of a few western Indian Ocean specimens with scaly maxillae that were otherwise indistinguishable from specimens he identified as *P. xanthura* that lacked scales on the maxillae. No scales were found on maxillae of either of the putative syntypes of *Caesio xanthura.*

Dr. Tetsushi Senta informed the first author (in litt., 12 Dec 1990) that while working in Singapore he noticed two kinds of *P. xanthura*; one had a scaly maxilla with the yellow band on the side restricted to the area above the lateral line; the other had a naked maxilla with the yellow band extending above and below the lateral line. (Senta *in* Kyushin et al. 1982:67 mentioned these two kinds of *P. xanthura.*) Specimens identified as *P. xanthura* with naked maxillae and the yellow band extending above and below the lateral line have been collected off Taiwan (Lee 1982:128, fig. 2) and southern Japan (Yoshino *in* Masuda et al. 1984:168; Masuda et al. 1984: pl. 154H).

At the request of Dr. Senta, one of his former students, Mr. Kiyoaki Kanashiro of the Okinawa Prefectural Fisheries Experimental Station, examined more than 5700 specimens identified as *P. xanthura* landed at the fishing port of Itoman from December 1985 to February 1987. All specimens examined by Mr. Kanashiro had naked maxillae. They could be separated into two size groups; one ranged from 180 to 350 mm FL (mode at 270–300 mm FL); the other, from 350 to 470 mm FL (mode at 400–410 mm FL). The first group made up 91% of the specimens examined, and in members of this group the yellow band was relatively wider below the origin of the soft dorsal fin than in specimens of the second group. Some fishermen operating out of Itoman distinguish the two groups of *P. xanthura,* and on occasion catch a few small individuals of the larger size group.

Dr. Phillip C. Heemstra informed the first author (in litt., 30 Jan 1991) of some observations made on *Paracaesio* (apparently *P. xanthura*) by Dr. Allan D. Connell, biologist/diver from Natal. Dr. Connell wrote Heemstra (19 Oct 1988) that while diving at Aliwal Shoal (off Umkomaas, near Durban, Natal) on the previous weekend, he observed a large school of *Paracaesio* overhead. The school included blue-gray and green (uniform olive-greenish gray, Heemstra, in litt., 30 Jan 1991) varieties. As Connell watched, a green individual descended to the bottom (a flat area on top of a reef where two wrasse [blue/black] maintained a cleaning station), and as the snapper became stationary, it suddenly turned silvery and then more slowly to the more familiar blue and yellow pattern. Later, two more individuals from the school went through similar color changes. Connell (undated, but 1985–1987) published a color photograph (pl. 95) of an underwater scene at Landers Reef (off Park Rynie, Natal) which is several kilometers south of Aliwal Shoal. In the middle of this photograph is a *Paracaesio* (labeled *P. xanthura* in the legend). According to Heemstra (in litt., 4 Apr 1991), this is the "uniform green *Paracaesio*" that is capable of changing color to the blue and yellow form. The individual depicted in Connell's photograph is mostly greenish gray with considerable blue on head and caudal fin (especially along dorsal margin of upper lobe) and yellow on distal margin of posterior part of soft dorsal fin and over most of caudal fin.

Data are inadequate to determine whether populations currently going by the name *Paracaesio xanthura* constitute a single variable, wide-ranging species or two (or more) species. Consequently, it seems best to continue recognizing a single species until specimens from the entire geographic range become available for study.

It is interesting to note, that in addition to the similarities in coloration shared by *P. xanthura* and the nominal *P. pedleyi* (see next subsection), that three caesionids, *Caesio cuning, C. teres,* and *C. xanthonota,* and two labracoglossids (scorpidids if one follows Johnson 1984), *Labracoglossa argentiventris* and *L. nitida,* have patterns of coloration that are very similar to that of *Paracaesio xanthura* (compare illustrations in Grant 1982:359, col. pl. 178; Masuda et al. 1984: pls. 135G, 154H; Carpenter 1987: pls. IA & D, VIA, D, & E; Carpenter 1988: 25, pl. I, figs. 43a, b, 44a, 45b; Randall et al. 1990:186), perhaps reflecting ecological similarities. All six (or seven) species have similar body forms; rather poorly developed jaw dentition; long, slender, fairly numerous gillrakers; and well-forked caudal fins—the kinds of adaptations expected in species feeding, at least part of the time, on plankton at some distance off the bottom. (Araga in Masuda et al. 1984:152 noted that *Labracoglossa argentiventris* is "somewhat similar" to *Caesio xanthonota* and *P. xanthura.*)

Paracaesio pedleyi.—The nominal species *P. pedleyi* resembles *P. xanthura* very closely in coloration. In the original description of *P. pedleyi,* McCulloch & Waite (1916: 442) stated that it "has the general characteristics of *P. xanthurus,*" but that it can be "distinguished by the form of the spinous dorsal and by the distribution of its colours." They wrote that "A dark band crosses the body between the middle of the spinous dorsal and the abdomen, . . ." in the holotype. Recently the first author examined the holotype (AMS I. 13885, 306 mm SL) of *P. pedleyi* from Lord Howe Island (off eastern Australia) and 11 other specimens (45–309 mm SL) from Australian waters that have been identified as *P. pedleyi*. The dark band mentioned by McCulloch & Waite (1916) was still evident on the holotype in mid-1991, and remnants of it are obvious on some of the other specimens identified as *P. pedleyi*; this band is not present in the putative syntypes of *Paracaesio xanthura* (RMNH 3948 & 5716) or in other examined specimens identified as this species. Grant (1982:359, in legend to col. pl. 178) reported that this band "intensifies after death." The spinous dorsal fin of the specimens identified as *P. pedleyi* appears to be more elevated anteriorly than in those identified as *P. xanthura*. There are a few other minor differences in measurements of body parts between specimens of the two nominal species and small differences in mean values for numbers of epipleural ribs (*P. xanthura*, 7–9, $\bar{X} = 7.7$, $n = 18$; *P. pedleyi*, 8–9, $\bar{X} = 8.4$, $n = 9$) and total numbers of gillrakers on the first arch (*P. xanthura*, 28–35, $\bar{X} = 31.3$, $n = 19$; *P. pedleyi*, 30–34, $\bar{X} = 32.1$, $n = 12$). Because of the small number of specimens examined, we defer judgment on the validity of *P. pedleyi* until a thorough study can be conducted.

Paracaesio tumida.—Tanaka (1917) described *Vegetichthys tumidus*, new genus and species, from a single specimen obtained from the Nagasaki fish market. Katayama (1934) placed *V. tumidus* in the synonymy of *V. xanthurus* (=*P. xanthura*). Although Abe & Shinohara (1962) recognized *P. tumida* as a valid species, recent authors have ignored it or considered it a junior synonym of *P. xanthura*. Because we have not examined the holotype of *V. tumidus* and because the original descriptions of the genus and species are in Japanese, we include here portions of an English translation, made in 1950 by Kiyomatsu Matsubara, of Tanaka (1917).

> Body length (to tip of upper lobe of caudal fin) 260 mm. Head $3\frac{1}{3}$ in body length (without caudal fin); depth $2\frac{4}{5}$. Eye $3\frac{1}{3}$ in head; interorbital space $2\frac{5}{7}$; snout 4.0; maxillary $2\frac{5}{7}$; depth of caudal peduncle $2\frac{5}{7}$. D. X, 9; A. III, 7; P. 17; branched caudal rays 15. Scales ctenoid, 66 along lateral line, 10 (above lateral line)—19 (below) in a transverse series. Vomer toothless; weak teeth present on palatines. Several rows of villiform teeth on jaws, outermost ones are canines—especially larger anteriorly. Caudal fin deeply forked. Color in formalin uniformly dark brown.

We have not examined any specimens of *Paracaesio* with 66 lateral-line scales (a count closer to the high count species of the genus—those with 68–73, than to the low count species—those with 47–50), nor have we encountered specimens of the genus with counts of dorsal soft rays or anal soft rays as low as nine and seven, respectively, although there are reports in the literature (e.g., Yoshino *in* Masuda et al. 1984:168) of nine dorsal soft rays for both *P. xanthura* and *P. sordida*. The low counts recorded for the holotype of *V. tumidus* may be the result of Tanaka's using methods for counting that are slightly different from ours. Species of *Paracaesio* typically have poorly developed vomerine dentition; in fact a few specimens that we have examined have almost no vomerine teeth and those present are very small. Accordingly, it is not surprising that Tanaka failed to detect any teeth on the vomer of the holotype of *V. tumidus*.

If *P. tumida* is not a valid species, the count of lateral-line scales and the presence of a deeply forked caudal fin in the holotype point to its being a synonym of either *P. xanthura* or *P. sordida*; both of these species, considering their known ranges, could have shown up in the Nagasaki market at the time the holotype of *P. tumida* was collected. Abe & Shinohara (1962:169–170) distinguished *P. tumida* from *P. sordida* on the basis of coloration, *P. tumida* having the dorsal part of the body and caudal fin yellow and the rest of the body blue—a pattern essentially that of *P. xanthura* (see subsection on *P. xanthura*). If the populations currently relegated to *P. xanthura* (see subsection on that species) actually represent two or more species, *P. tumida* may be the correct name for one of them. (It should be emphasized that we lack information on live coloration and maxillary squamation for the holotype of *V. tumidus*.) Considering the similarities in coloration between *P. tumida* (as presented by Abe & Shinohara 1962) and *P. xanthura* and despite the low counts for lateral-line scales and dorsal and anal soft rays given by Tanaka (1917), we consider it best to continue recognizing *Vegetichthys tumidus* Tanaka, 1917, as a junior synonym of *Paracaesio xanthura* (Bleeker, 1869) until the populations of *P. xanthura* have been adequately studied.

Paracaesio cantharoides.—Aetiasis cantharoides Barnard, 1937, new genus and species, was described from a specimen collected off the coast of Natal, South Africa. Barnard (1937) stated that the single specimen (no catalogue number given, 400 mm in length) upon which the species description was based was obtained by the SAM through "the kindness of Mr. C. L. Biden." The first author has examined a specimen of *Paracaesio* (SAM 18430, ca. 395 mm FL, 355 mm SL) taken off Durban, Natal, that was transferred to the SAM collections from the Hastings collection by C. L. Biden in 1933. Barnard's specimen of *A. cantharoides* had scales on the maxilla and was dissected on the right side of the head to study the morphology of the vomer, palatines, pharyngeal bones, and jaws. The specimen of *Paracaesio* from the SAM (SAM 18430) has scales on the left maxilla and has had the right side of the head dissected. In addition, a glass tube accompanying the specimen contains the bones depicted in Barnard's (1937:60, text-fig. 2) illustration, although Barnard's drawings are not entirely accurate representations of the bones in the glass tube. Barnard provided no information on live coloration and there is no evidence of live coloration remaining on SAM 18430. Although there are some discrepancies between Barnard's description and SAM 18430 (e.g., counts of dorsal-fin rays and branchiostegal rays), we believe that SAM 18430 is the holotype of *Aetiasis cantharoides* because the deposition of the specimen, source and length of the specimen, evidence of dissection, and the disarticulated head bones with the specimen match the information provided in Barnard's description and because there appears to be no other specimen in the collections of the SAM that could be the holotype. In addition, the drawing of the head and anterior part of the body accompanying the original description of *A. cantharoides* in Barnard (1937:60, text-fig. 2) is of a *Paracaesio*.

Abe and Shinohara (1962) recognized *Paracaesio cantharoides* as a valid species, apparently largely on the basis of the presence of scales on the maxilla. Anderson (1987) considered *P. cantharoides* as a junior synonym of *P. xanthura* because he examined a few western Indian Ocean specimens with scaly maxillae that were otherwise indistinguishable from *P. xanthura* (see subsection on *P. xanthura*).

We believe SAM 18430 to be the holotype of *Aetiasis cantharoides* and that further study could show *P. cantharoides* to be a valid species. Therefore, we offer the following descriptive information on SAM 18430: SL 355 mm; dorsal-fin rays X, 10; anal-fin rays III, 8; pectoral-fin rays 17 (both sides); gillrakers 7 + 21—total 28; tubed lateral-line scales 70 (left) 71 (right); cheek-scale rows 7 (both sides); predorsal scales ca. 24; scales between origin of dorsal fin and lateral line 10; scales between origin of anal fin and lateral line 18; scale rows between middle of spinous dorsal fin and lateral line 6½; circum-caudal-peduncle scales 28; maxilla with scales; caudal fin damaged, but clearly well forked.

Presently, it seems best to consider *Aetiasis cantharoides* Barnard, 1937, a junior synonym of *Paracaesio xanthura* (Bleeker, 1869).

Sexual Dimorphism

Mr. William A. Roumillat examined histological sections of the gonads of the ten specimens identified as *P. pedleyi* (may = *P. xanthura*) that have anterior jaw teeth that are large enough to measure with some degree of precision. With the exception of the upper jaw teeth of one male (247 mm SL), the six males (170–307 mm SL) have slightly longer longest anterior jaw teeth than do the four females (216–309 mm SL), suggesting that tooth size may be sexually dimorphic in *P. pedleyi* (measurements in percentages of postorbital head length: longest upper jaw tooth:—males 3.2–5.9, $\bar{X} = 4.6$—females 3.5–4.1, $\bar{X} = 3.8$; longest lower jaw tooth:—males 3.4–4.9, $\bar{X} = 4.0$—females 2.6–3.2, $\bar{X} = 2.9$). If tooth size is sexually dimorphic in *P. pedleyi,* it is the first external character recognized as such in the Lutjanidae. Too few data are available to determine if there is a correlation between tooth size and sex in other species of *Paracaesio.*

Relationships

The genus *Paracaesio,* as currently understood, consists of about eight or nine very similar species that possess what can be called the "*Paracaesio* look." Despite the fact that these species appear to form a group of closely related species, we know of no synapomorphy uniting them. Two characters, possibly correlated, relative lengths of last two dorsal soft rays and relative lengths of last two anal soft rays, may be synapomorphic, but we lack data to demonstrate this convincingly.

Because we have examined specimens of all nominal species of *Paracaesio* (except *P. tumida*), we offer the following comments on relationships. The evidence suggests that among the Lutjanidae, in general, and the Apsilinae, in particular, that increased numbers of lateral-line scales, barred color pattern in adults, and scaly maxillae are derived conditions. If these character states are synapomorphic, three monophyletic groups of species are recognizable: *P. paragrapsimodon, P. sordida, P. waltervadi,* and the *P. xanthura* complex (with increased numbers of lateral-line scales); *P. gonzalesi, P. kusakarii,* and *P. stonei* (adults with barred color pattern); and *P. gonzalesi* and *P. kusakarii* (with scaly maxillae). A more definitive statement on the relationships of these species will be possible only after much additional study.

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Addendum

In May 1992, while in residence as a research fellow at the J. L. B. Smith Institute of Ichthyology in Grahamstown, Republic of South Africa, the first author examined an unusual specimen (RUSI 14863, 391 mm SL, from Aliwal Shoal, Natal) with patterns of dentition and coloration previously unobserved by us in *Paracaesio.* This individual has about six irregular rows of enlarged, strongly exserted caniniform teeth at the anterior ends of the dentaries. The other teeth in both jaws are quite small. The longest of these exserted caniniform teeth is 5.9% snout length, 4.2% postorbital head length, appreciably shorter than the longest lower jaw teeth in *P. paragrapsimodon.* No information is available on live coloration, but in alcohol the specimen is dark dorsally, lighter ventrally. In addition, on the right side only, there is a narrow oblique dark bar running from near bases of first and second anal soft rays anterodorsally to blend into dark background of dorsum of body; anterior to this oblique bar, hints of other oblique bars are visible. There are two rows of small scales on each preopercle peripheral to and distinctly separated from the main group of cheek scales; this is reminiscent of the preopercular squamation of *P. sordida.* Other data for this specimen are: dorsal fin rays X, 10; anal-fin rays III, 8; pectoral-fin rays 17 (both sides); gillrakers 9 + 20—total 29; tubed lateral-line scales 71 (left), ca. 72 (right); maxilla without scales; caudal fin damaged but apparently forked.

Dr. Phillip C. Heemstra received a color transparency of a specimen of *Paracaesio* from Mr. Simon Chater of the Oceanographic Research Institute, Durban, Natal, and subsequently gave it to the first author. In a letter, dated 23 April 1992, Chater wrote Heemstra that the specimen was collected in 40 m off Inhaca Island [Mozambique] and that when freshly caught "it was coppery bronze with two broad powder blue stripes running laterally from just behind the gill flap to base of the peduncle where they converged." Examination of the transparency shows the coloration to be similar to that described in Chater's letter, about 70 tubed lateral-line scales, and a well-forked caudal fin. We have not seen this pattern of coloration previously in *Paracaesio.* Unfortunately, the specimen was not preserved.

With the information available, it is impossible to determine the status of the specimen from Aliwal Shoal (RUSI 14863) or that of the specimen caught off Inhaca Island.

The first author expresses his gratitude to the staff, particularly P. C. Heemstra, of the J. L. B. Smith Institute of Ichthyology for providing space, facilities, and assistance from May through July 1992, and to the Foundation for Research Development, Republic of South Africa, for the award of a research fellowship.

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A NEW SPECIES OF *SPHOEROIDES* PUFFERFISH (TELEOSTEI: TETRAODONTIDAE) WITH EXTENSIVE HYPEROSTOSIS FROM THE PLIOCENE OF NORTH CAROLINA

James C. Tyler, Robert W. Purdy, and Karl H. Oliver

Abstract.—The relatively intact skull of a tetraodontid pufferfish from the Yorktown Formation (Unit 3 of Lee Creek Mine) of the Pliocene of eastern North Carolina (ca. 5 MYA) represents a new species of *Sphoeroides* from a coastal marine habitat of about 50–80 meters depth. It differs from all of the other species (18 Recent and one fossil) of the genus in the configuration of the bones forming the rim of the upper orbit, the shape of the posterior end of the frontal and the presence of extensive hyperostosis of the opercular bones and ventral postcleithrum. This is the first report of hyperostosis in *Sphoeroides.* With the evidence from the hyperostotic skull, it is reasonable to assume that most of the thousands of previously unidentified, disarticulated, and hyperostotic opercular and cleithral bones that characterize Unit 3 of the Yorktown Formation are the remains of the new species, *S. hyperostosus.* These bones represent specimens ranging in body size from about 80 to 500 mm SL; only four of the 19 other species of *Sphoeroides* reach sizes approaching 250 mm SL.

Skeletal remains, varying from nearly intact whole skeletons to disarticulated parts, of a wide variety of elasmobranch and teleost fish families have been found in Units 1, 2, and 4 basal parts of the Yorktown Formation of the Pliocene of Beaufort County, eastern North Carolina, at Lee Creek Mine. By contrast, Unit 3 of the Yorktown at Lee Creek has few even partial fish skeletons, but a richness of otoliths belonging to 45 taxa in 17 teleost families (Fitch & Lavenberg 1983) and thousands of disarticulated hyperostotic (swollen) bones whose identity has remained a mystery. Some of these hyperostotic bones have been described and illustrated (Weiler 1973), but only with incorrect guesses as to what bones they represent and no identification to taxa other than presumed teleost.

In 1987, a relatively complete skull (Fig. 1) of a tetraodontid pufferfish was recovered by Mr. Craig Healy from Unit 3 at Lee Creek Mine. It has hyperostotic opercular bones that match the thousands of comparable disarticulated bones from that unit.

Among the approximately 16 genera of tetraodontids surveyed by Tyler (1980), the features of the Pliocene skull are most similar to those found in the speciose genus *Sphoeroides,* especially in: the moderate length and width of the ethmoid; and the anteriorly tapering frontals widely separating the lateral ethmoids and sphenotics, forming the border of the middle of the top of the orbit. The similarity of the Pliocene skull from North Carolina to *Sphoeroides* is not surprising since *Sphoeroides* is one of the two genera of tetraodontids occurring today along the Atlantic coast of North America. The other is *Lagocephalus,* in which the skull has a long posterolateral extension of the frontal contacting the pterotic to roof over a fossa, and a long and broad ethmoid. These specialized features of *Lagocephalus* are not present in the Pliocene skull.

Even while basically similar to *Sphoeroides,* the Pliocene skull differs from those of the 18 extant and the only other fossil species of that genus not only by the presence of hyperostosis, which is absent in all of the other species, but also by the configuration of the lateral ethmoid, frontal, and sphenotic, by the degree that the frontal and sphenotic roof over the posterodorsal region of the orbit, and by uniquely structured posterior flanges of the frontals. This degree of osteological difference between the hyperostotic fossil species and all of the other species is much greater than that between most of the species of relatively similar skull width, but it is about the same degree of difference as that between the species at the ends of the extremes of skull width.

While the presence of swollen, gall-like hyperostotic fish bones has often been considered as a tumorous pathology, we accept current evidence that it is a normal condition in those few species in which it occurs and that it can be species specific in the pattern of bones affected (W. F. Smith-Vaniz, pers. comm. based on manuscript reviewing fish hyperostosis and investigations on the histology and growth of hyperostotic bone). For example, some jacks of the genus *Caranx* that are extremely difficult to distinguish externally exhibit markedly different and consistent patterns of hyperostosis. Therefore, it would be reasonable to describe the Pliocene skull as a new species of *Sphoeroides* on the basis alone of the unique hyperostosis of the opercular bones. Because of our confidence that this hyperostosis is normal and species specific, we name the new species from the Pliocene *Sphoeroides hyperostosus* to call attention to one of its major features of difference from all other species of that genus.

Sphoeroides hyperostosus is known only from the Lee Creek locality that during the Pliocene was a coastal marine habitat estimated to have been of about 50 to 80 m depth (Gibson 1967:646). The skull of *S. hyperostosus* has many general features similar to the common northern puffer, *S. maculatus,* that occurs in shallow coastal waters (usually less than 35 m) of the mid-Atlantic states. However, the skull of *S. hyperostosus* also has a few specialized features similar to the more rarely collected blunthead puffer, *S. pachygaster,* a deeper water (usually more than 100 m) species of almost circumglobal distribution. We hypothesize below on the basis of osteological peculiarities that *S. hyperostosus* is most closely related to *S. pachygaster* and that they together are most closely related to the *S. maculatus-nephelus-parvus-tyleri* species complex defined by Shipp (1974:128–129).

The disarticulated hyperostotic opercular bones that are so common at Lee Creek Mine can reasonably be assumed to be from *S. hyperostosus* because of their similarity to those in the Lee Creek skull. We presume that the disarticulated hyperostotic ventral postcleithra from Lee Creek Mine also are from *S. hyperostosus* simply because it is the only species of *Sphoeroides* (and tetraodontid) known from Lee Creek and the disarticulated ventral postcleithra in general are similar to those of most species of *Sphoeroides.* This assumption is strengthened by the disarticulated ventral postcleithra being relatively broad in the middle region, an unusual feature also found in *S. pachygaster* to which we think *S. hyperostosus* is most closely related.

Methods

The holotypic skull was relatively free of substrate when discovered and was subsequently prepared only to the extent of removing small amounts of substrate from the external surfaces of the exposed bones. The first four vertebrae were attached to the rear of the skull when it was recovered, but the second to fourth vertebrae became detached during preparation. After photographing the skull, with only the first vertebra attached, the premaxilla and dentary from the right side were removed in order to examine the medial surface of these beak-like bones.

Measurements are recorded to nearest 0.1 mm, but given to nearest whole number for measurements over 100 mm. Body length is standard length (SL). Cranial length is from front of palatine to rear of part of cranium formed by exoccipital-epiotic-pterotic to either side of supraoccipital, excluding supraoccipital flange and posterolateral pterotic flange. Interorbital width is least width, just behind lateral ethmoids. Opercle length is from uppermost point on dorsolateral flange above articular head to ventral point. Preopercle length is from anteroventral to posterodorsal points. Subopercle length is greatest anteroposterior distance, not dorsoventral; subopercle thickness is greatest distance between medial and lateral surfaces. Ventral postcleithrum length is between tapering end points above and below. Dentary and premaxillary length is from anteromedially to posterolaterally.

Materials are from the collections of the National Museum of Natural History (USNM), Paleontological Institute, Moscow (PIN), Academy of Natural Sciences of Philadelphia (ANSP), and the Florida State University (FSU).

Analysis of relationships is phenetic and osteological features are considered specialized within *Sphoeroides* if they do not occur in other tetraodontid genera thought to be related to it in this family for which there is no cladistic analysis available.

Materials

Fossil species.—

Sphoeroides jamestyleri Bannikov: PIN 287-9, holotype, 22.6 mm SL, in part and counterpart, Kerch Peninsula, Crimea, southern Ukraine, Tarkhan Horizon, lower Miocene; PIN 3974-8, paratype, ca. 60 mm SL, skull in dorsal view and distorted axial skeleton, single plate; plus uncatalogued piece of caudal skeleton not designated as type material; all with same data as holotype.

Extant species (cleared and stained specimens, unless otherwise noted).—

Sphoeroides angusticeps (Jenyns): ANSP 95841, 1, 172 mm.

Sphoeroides annulatus (Jenyns): ANSP 109459, 3, 15.0–21.4 mm; ANSP 109461, 3, 10.9–15.8 mm; ANSP 109460, 1, 13.5 mm; ANSP 109458, 1, 174 mm.

Sphoeroides dorsalis Longley: ANSP 109462, 1, 131 mm; ANSP 109519, 1, 139 mm (dry skeleton); ANSP 109520, 1, 155 mm (dry skeleton).

Sphoeroides formosus (Günther): ANSP 95552, 1, 175 mm (often recognized in the monotypic genus *Guentheridia*).

Sphoeroides georgemilleri Shipp: ANSP 117319, 1, 88.4 mm (paratype).

Sphoeroides greeleyi Gilbert: ANSP 109463, 3, 24.2–60.8 mm.

Sphoeroides lobatus (Steindachner): ANSP 97332, 1, 67.5 mm.

Sphoeroides maculatus (Bloch & Schneider): ANSP 109466, 1, 126 mm; ANSP 109464, 2, 97.5–106 mm; ANSP 109467, 1, 201 mm. Dry skeletons: ANSP 16793, 1, 172 mm; ANSP 109552, 1, 171 mm; USNM 283611, 1, 205 mm; USNM 163742, 1, 188 mm; USNM 12986, 1, 172 mm; USNM 273171, 1, 139 mm. Alcohol preserved (top of skull examined with skin laid aside): USNM 75162, 1, 225 mm; USNM 42481, 1, 210 mm; USNM 75161, 1, 206 mm; USNM 315196, 2, 169–182 mm; USNM 93847, 1, 174 mm; USNM 14827, 2, 153–175 mm; USNM 42476, 1, 110 mm; USNM 25689, 1, 147 mm; USNM 28750, 1, 150 mm; USNM 163742, 1, 157, mm; USNM 50891, 1, 160 mm; USNM 51869, 1, 171 mm; USNM 74873, 1, 161 mm; USNM 61468, 2, 122–142 mm; USNM 156489, 2, 87.2–110 mm; USNM 315195, 4, 74.5–101 mm. Radiographs: USNM 75162, 1, 225 mm; USNM 42481, 210 mm; USNM 75161, 1, 206 mm; USNM 315196, 2, 169–181 mm; USNM 14827, 2, 153–175 mm; USNM 93847, 1, 174 mm; USNM 28750, 1, 150 mm; USNM 25689, 1, 147 mm; USNM 42476, 1, 110 mm; USNM 4638, 4, 74.3–184 mm; USNM 156489, 2, 86.7–109 mm; USNM 156477, 2, 63.5–78.4 mm;

USNM 118348, 5, 66.2–108 mm; USNM 155996, 1, 78.6 mm; USNM 156478, 1, 85.3 mm; USNM 156523, 1, 64.1 mm; USNM 155988, 1, 125 mm; USNM 91107, 1, 132 mm; USNM 155843, 1, 122 mm; USNM 36016, 1, 98.7 mm; USNM 143012, 5, 25.1–34.6 mm.

Sphoeroides marmoratus (Lowe): ANSP 106505, 1, 98.4 mm.

Sphoeroides nephelus (Goode & Bean): ANSP 105222, 1, 48.5 mm; ANSP 110533, 1, 128 mm.

Sphoeroides pachygaster (Müller & Troschel): Cleared and stained: ANSP 109468, 2, 134–137 mm; ANSP 104781, 1, 117 mm; ANSP 101322, 1, 80.6 mm. Alcohol preserved (top of skull examined with skin laid aside): USNM 42143, 1, 218 mm; USNM 121952, 1, 159 mm; USNM 307615, 1, 129 mm; USNM 307615, 1, 127 mm. Radiograph: USNM 42143, 1, 218 mm.

Sphoeroides parvus Shipp & Yerger: USNM 120084, 2, 38.7 and 80.3 mm. Radiographs: USNM 203248, 1, 79.7 mm (holotype); USNM 156492, 3, 62.8–84.9 mm.

Sphoeroides sechurae Hildebrand: USNM 128123, 1, 56.3 mm (paratype).

Sphoeroides spengleri (Bloch): Dry skeletons: ANSP 10531, 1, ca. 90 mm; ANSP 10532, 1, 92.8 mm.

Sphoeroides testudineus (Linnaeus): ANSP 107328, 1, 68.5 mm.

Sphoeroides trichocephalus (Cope): ANSP 109742, 1, 57.1 mm.

Sphoeroides tyleri Shipp: USNM 227198, 2, 51.6 and 73.4 mm.

Sphoeroides yergeri Shipp: FSU 25256, 1, 59.5 mm (paratype).

Lagocephalus inermis (Temminck & Schlegel): ANSP 100832, 1, 52.2 mm. Radiograph: USNM 207052, 1, 334 mm.

Lagocephalus laevigatus (Linnaeus): ANSP 103120, 1, 61.4 mm; ANSP 102155, 2, 143–166 mm. Dry skeleton: ANSP 102154, 1, ca. 290 mm. Wet disarticulated skeleton: ANSP 102153, 1, ca. 290 mm. Radiographs: USNM 120066, 1, 232 mm; USNM 37689, 1, 279 mm; USNM 76680, 1, 329 mm; USNM 22807, 1, 386 mm; USNM 20757, 2, 145–148 mm; USNM 156515, 1, 121 mm; USNM 15632, 1, 112 mm; USNM 156531, 1, 118 mm; ANSP 207052, 1, 334 mm; ANSP 78225, 1, 419 mm; ANSP 78235, 1, 312 mm; ANSP 102154, 1, ca. 300 mm.

Lagocephalus lagocephalus (Linnaeus): ANSP 70299, 1, 214 mm.

Lagocephalus lunaris (Bloch & Schneider): ANSP 111509, 1, 62.3 mm.

Lagocephalus scleratus (Gmelin): ANSP 96685, 1, 80.9 mm.

Lagocephalus spadiceus (Richardson): ANSP 104787, 1, 98.2 mm.

Tetraodontidae (sensu Tyler, 1980)

Sphoeroides Anonymous (Lacepède, 1798) (as defined by Fraser-Brunner 1943, Shipp & Yerger 1969, Shipp 1974, Tyler 1980, and Tyler & Paxton 1979).

Sphoeroides hyperostosus, new species

Type specimens and horizon.—USNM 437601, holotype, relatively complete skull and first four vertebrae, 72.5 mm cranial length, original number 378527, Lee Creek Mine, Aurora, Beaufort County, North Carolina, Unit no. 3 of the Yorktown Formation, lower Pliocene, about 5 MYA, collected 5 December 1987 by Craig Healy; USNM 290643, paratype, incomplete cranium, 37.0 mm greatest length, same locality as holotype. All of the following are disarticulated hyperostotic bones in the USNM Lee Creek Osteichthyes collection, most of which are uncatalogued. Most of the catalogued pieces are in the 283, 288 and 440 thousand series. All bones illustrated here have been catalogued. The four most common disarticulated bones in the collection referable to *S. hyperostosus* but not designated as type specimens are: 1047 ventral postcleithra, 19.7 to 70.8 mm; 734 subopercles, 12.1–39.6 mm; 712 preopercles, 18.5–56.5 mm; 211 opercles, 16.4–40.6

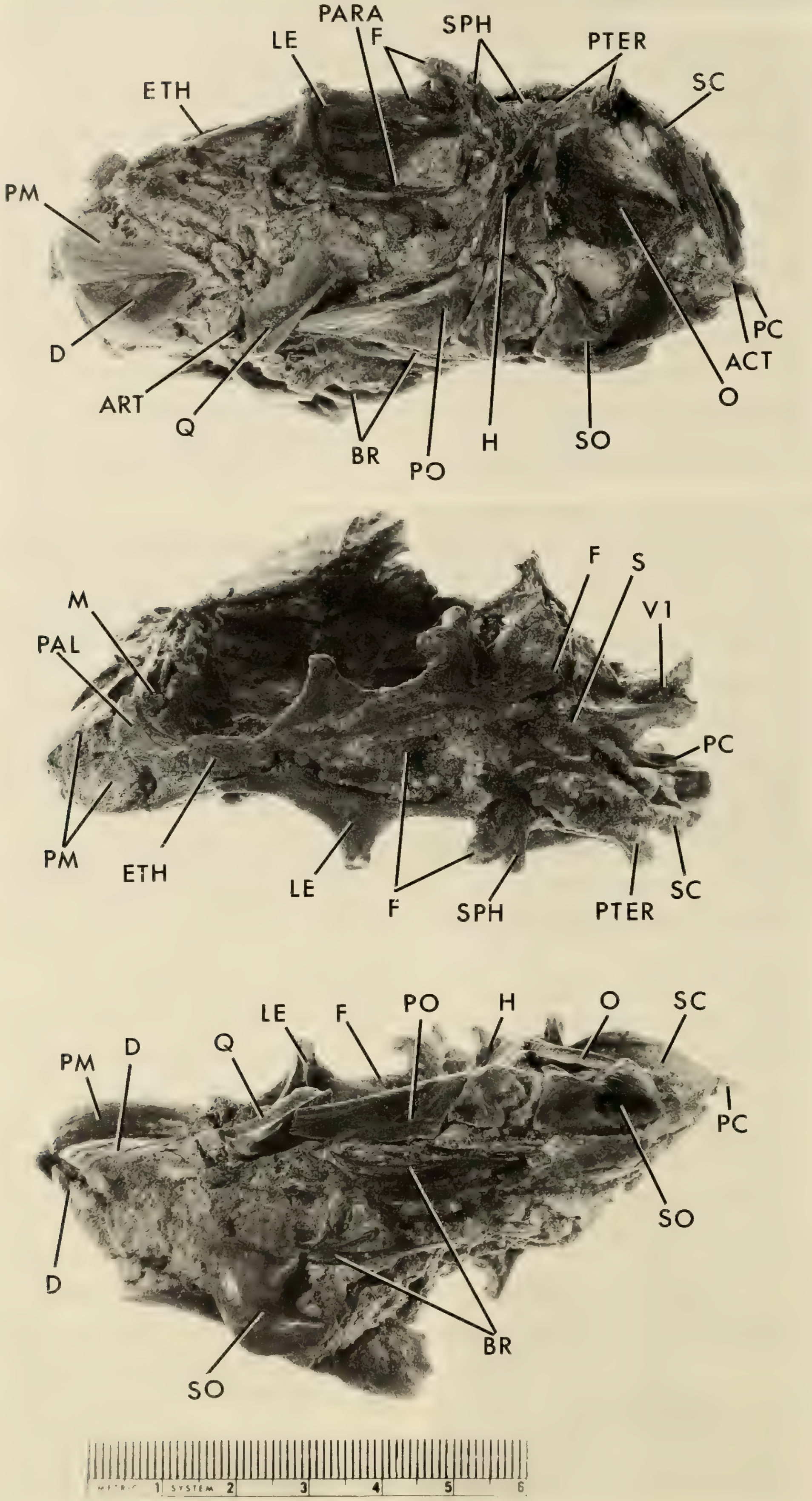

Fig. 1. *Sphoeroides hyperostosus,* USNM 437601, holotype, Pliocene of the Yorktown Formation, Lee Creek Mine, North Carolina, 72.5 mm cranial length, lateral (above), dorsal (middle) and ventral (below) views of the skull, representing a fish of about 240 mm SL. Abbreviations for the names of the bones here and in other

mm. Additionally, there are 8 dentaries, 19.6–27.7 mm, and 7 premaxillae, 17.3–30.4 mm.

Etymology.—Hyper, a great amount, and *ostosus,* bony growth; for the normally swollen bones; masculine.

Diagnosis.—Differs from all other species of *Sphoeroides* by the: hyperostosis of the opercle, subopercle, preopercle, and ventral postcleithrum; lateral ethmoid with a broad flat unornamented upper surface, without an obliquely sloping anteroventral edge, the flange formed by the frontal and sphenotic at the posterodorsal region of the orbit directed anterolaterally, increasing the amount of roofing over the orbit; the posterior region of the dorsal surface of the frontal with a thick curved crest that extends posteriorly as a short process over the epiotic.

Description.—Most of the bones of the skull of the holotype (Fig. 1) are present on one side or the other. On the left (more complete) side of the skull the only bone missing is the maxilla. The maxilla is present, however, on the right side. The pectoral girdle on the left side is represented by the supracleithrum, dorsal postcleithrum, some of the actinosts and the dorsal region of the coracoid-scapula, and, internal to the latter and not exposed in lateral view, the cleithrum (which can be seen clearly in medial view). The pterygoid series is present on both sides but the limits of the individual bones are unclear. The branchiostegal rays are present on the left side, with the enlarged first ray that forms the specialized tetraodontid pumping plate well exposed. The opercular series is missing from the right side, as is the pectoral girdle except for some pieces of the cleithrum. The pterotic on the right side is displaced forward.

The roof of the skull is distorted by a longitudinal fracture along much of the length of the frontal and ethmoid on the left side. The portions of the skull to either side of the fracture are slightly separated from one another and slightly displaced anteroposteriorly relative to one another. The amount of separation, displacement, and artificial widening of the skull has been taken into account and adjusted for in the dorsal view reconstruction of the skull and in the measurement of the interorbital width.

The paratypic skull (Fig. 2) is far less complete and much abraded. It represents the top of the neurocranium, with the rear portion missing, the lateral processes of the lateral ethmoids abraded, especially on the left side, the front of the ethmoid-vomer missing, the frontals incomplete posteriorly, the lateral processes of the frontal and sphenotic in the posterodorsal region of the orbit abraded, and most of the supraoccipital and epiotic region, along with the pterotic, missing. The greatest length of the incomplete cranium is 27.0 mm. What remains of the top of the cranium of the paratype is entirely consistent with the structure in the larger and better preserved holotype, including a comparable interorbital width (13.7 mm) relative to the approximate length and width of the cranium. The descriptions of the skull that follow are based on the holotype unless otherwise stated.

The upper and lower jaws (Figs. 1 and 4) are typical for a tetraodontid, and a single rounded trituration or internal mastication tooth is present posteromedially on the inner surface of each premaxilla. The palatine broadly interlocks with the vomer medially and posteriorly, whereas the vomer underlies the anterior region of the ethmoid, which

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figures: ACT—actinost; ART—articular; BR—branchiostegal ray; D—dentary; ETH—ethmoid; EO—exoccipital; EPI—epiotic; F—frontal; H—hyomandibula; IO—interopercle; LE—lateral ethmoid; M—maxilla; O—opercle; PAL—palatine; PARA—parasphenoid; PC—postcleithrum (dorsal); PM—premaxilla; PO—preopercle; PTER—pterotic; Q—quadrate; S—supraoccipital; SC—supracleithrum; SPH—sphenotic; SO—subopercle; V—vomer; V1—first vertebra.

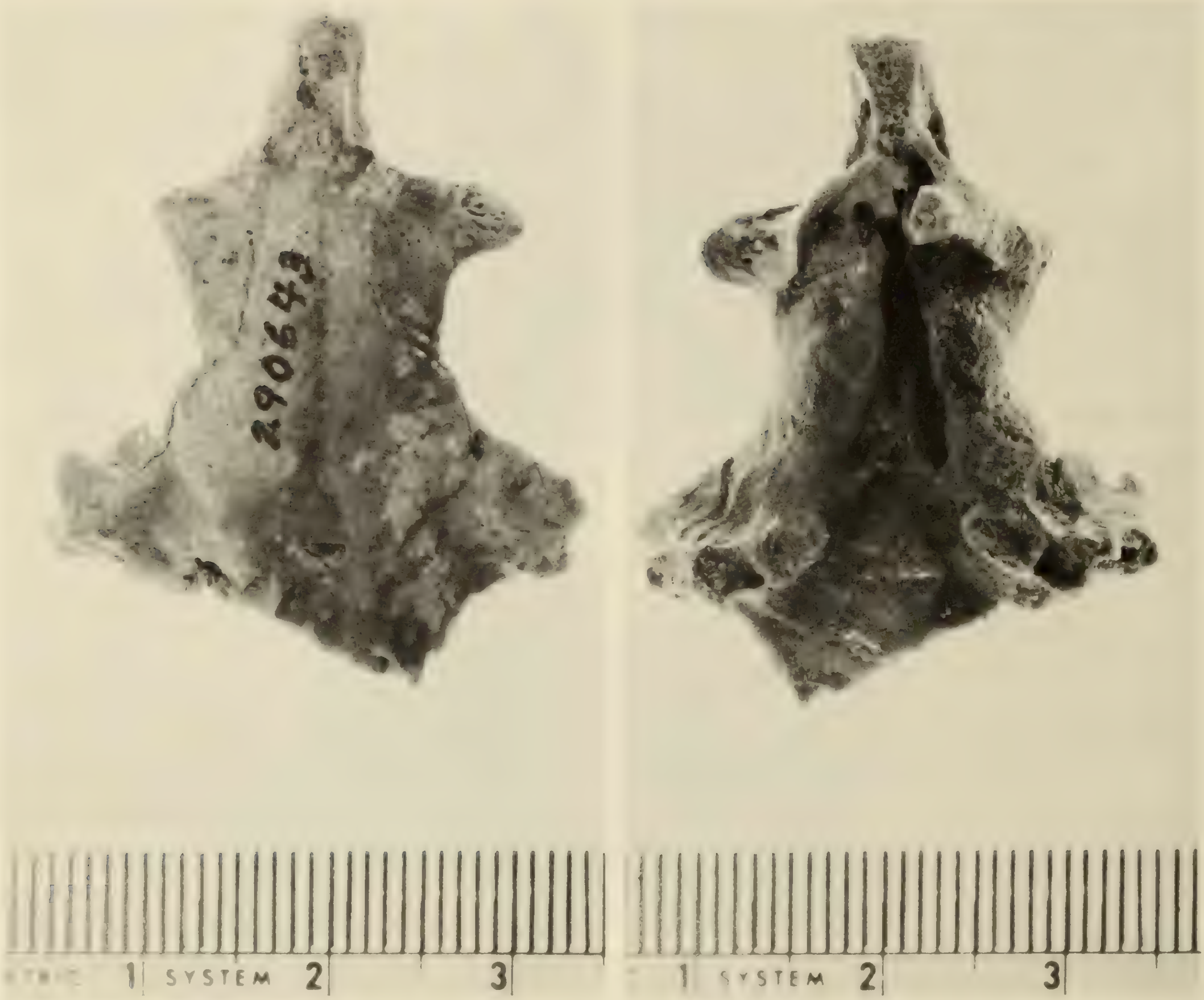

Fig. 2. *Sphoeroides hyperostosus,* USNM 290643, paratype, Pliocene of the Yorktown Formation, Lee Creek Mine, North Carolina, 37.0 mm greatest length of the much abraded incomplete cranium; dorsal view to left, ventral view to right.

is of moderate width. The lateral ethmoids are robust and have a broad flat upper surface without an obliquely sloping anterolateral region to accommodate the nasal apparatus; rather, the flat anterolateral edge extends out as a roof over this area.

The frontals taper to an indistinct point in the region between the anterior ends of the dorsal surface of the lateral ethmoids. The frontals are somewhat upraised where they form the lateral margin of the middle of the upper region of the bony orbit, widely separating the lateral ethmoids and sphenotics. Just behind the orbit the frontal and sphenotic form a strong laterally and slightly anteriorly directed process. This process increases the amount of roofing over the posterodorsal region of the orbit and decreases the distance between the frontal-sphenotic flange and the lateral wing of the lateral ethmoid. The upraised interorbital margin of the frontal continues posteriorly as a thick ridge that curves medially to the region in front of the supraoccipital and then curves posterolaterally to form a process that extends out slightly above the epiotic as a short narrow roof over the anterodorsal region of that bone.

The pterotic has a strong lateral process in the region between its articulation with the hyomandibula and supracleithrum. The limits of the anterior region of the supraoccipital between the posterior flanges of the frontals are indistinct, but the supraoccipital crest is well preserved, projecting posteriorly between the bifid neural arch of the first vertebra. The supracleithrum is robust, with a laterally expanded posterior edge and a thinner anterior flange. The dorsal postcleithrum, expanded in the middle and tapering at both ends, articulates anterodorsally along the medial surface of the upper end of the cleithrum (not exposed in lateral view), whereas its posteroventral end (only slightly exposed in lateral view), which would articulate with the missing ventral postcleithrum, lies just behind the region of the indistinct remains of the hour glass-shaped actinosts and coracoid-scapular complex.

The opercle is slightly hyperostotic, about as much so as most of the disarticulated opercles from Lee Creek. The dorsal end of the opercle forms a head for articulation with the upper posterior edge of the hyomandibula, while the opercle is incomplete ventrally where it would overlie the subopercle.

The subopercle is moderately hyperostotic, less so than most of the disarticulated subopercles of comparable size, but with about the same degree of swelling as in the three bones numbered 364322, 364227 and 440859 in Fig. 3. The posterodorsal lobe of the subopercle behind the dorsal indentation for articulation with the opercle is slightly longer and has a more oblique edge facing the ventral flange of the opercle than is the case with the anterodorsal lobe, whereas the anteroventral edge of the subopercle is more acute than the rounded posteroventral edge. The groove on the subopercle at the bottom of its dorsal indentation to accommodate the opercular flange is on the lateral surface. These asymmetries are useful in determining which of the disarticulated subopercles are from the left versus right side of the skull.

The hyomandibula has a sturdy upper portion of triangular shape in lateral view for articulation with the cranium (sphenotic in front and pterotic behind in lateral view) and a lower shaft-like portion, demarked from the upper by a thick crest horizontally along its surface, supporting the dorsal region of the opercle. The preopercle is moderately hyperostotic, less so than most of the disarticulated preopercles of comparable size, but with about the same degree of swelling as in the largest of the preopercles in Fig. 3. The preopercle is much fractured but has an entirely normal tetraodontid shape and articulation along the ventral shaft of the hyomandibula and ventral edge of the quadrate.

The quadrate is displaced anteroventrally but obviously when complete had a typical tetraodontid shape and articulation with the preopercle posteroventrally, the pterygoid bones dorsally and the articular anteriorly. The limits of the pterygoid bones are not well preserved, but everything that is evident is typical of tetraodontids and *Sphoeroides,* including a large, posteriorly rounded metapterygoid and a vertically oriented mesopterygoid contacting the region of articulation between the vomer and lateral ethmoid. The remains of a rod-like interhyal are evident behind the fractured and displaced regions of the quadrate and anterior end of the preopercle.

The parasphenoid is a strong shaft under the orbit; its ventral flange is not exposed. Anteriorly the parasphenoid supports the thick ventral shaft of the lateral ethmoid, while posteriorly its dorsolateral flanges meet the prootics. The prootics have medial flanges forming a partial roof over at least the anterior region of the myodome. The parasphenoid lacks a dorsal lobe in the interorbital septum that in some tetraodontids contacts the frontals.

Measurements of the holotype are: cranial length 72.5 mm; least interorbital width 15.2 mm when corrected for fracture (interorbital width into cranial length 4.8 ×); supracleithrum length 30.4 mm; subopercle length, horizontally from anterior to pos-

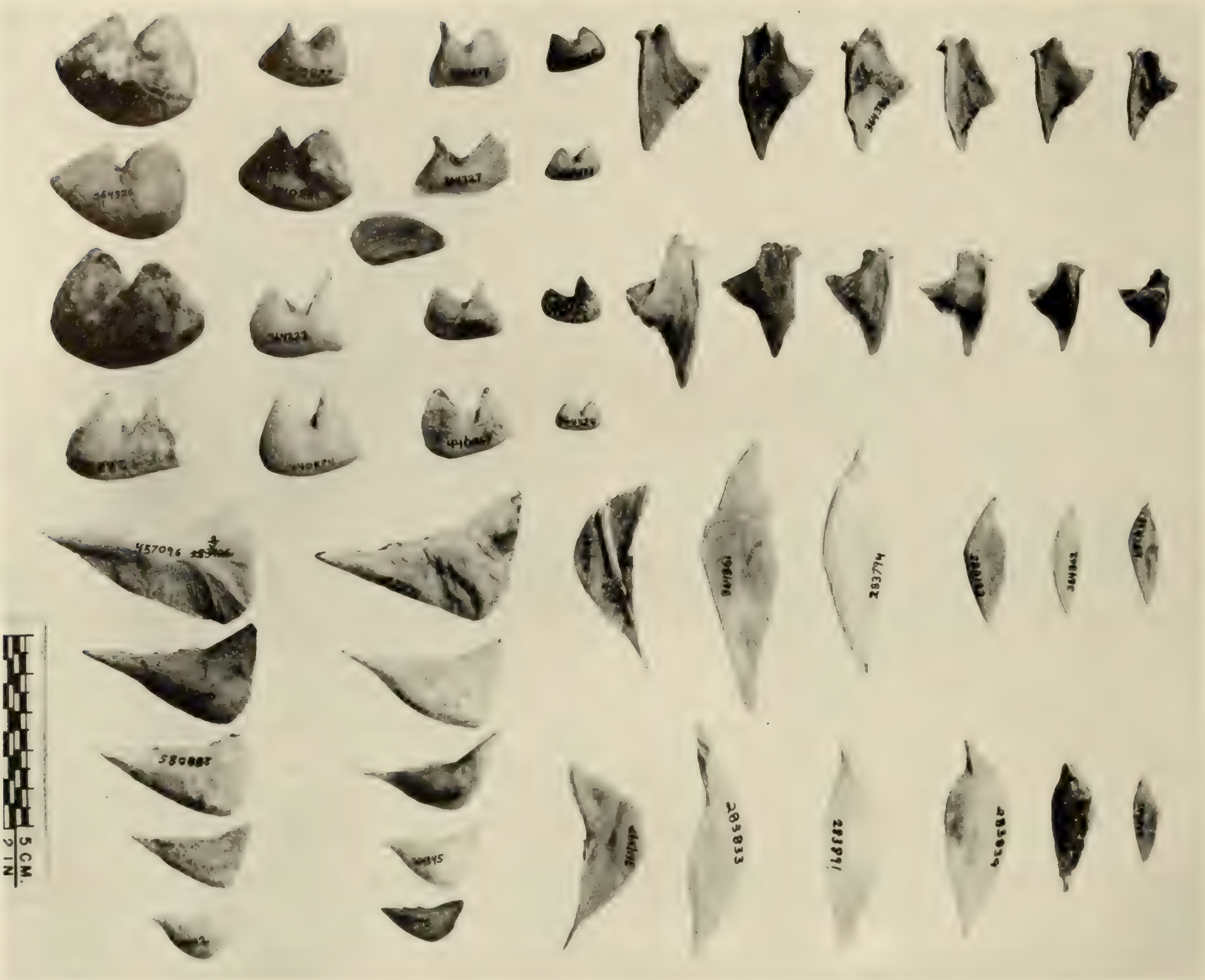

Fig. 3. *Sphoeroides hyperostosus,* a selection of disarticulated hyperostotic bones from Lee Creek Mine, showing most of the range in size and variation in degree of hyperostosis. All bones in lateral view unless otherwise stated. Upper left, subopercles: upper two horizontal rows, left side; lower two horizontal rows, right side; in middle, a section through middle of horizontal length of one of the subopercles; range in horizontal length 12.1 to 39.6 mm. Lower left, preopercles: two vertical rows to left, left side; two bones to right, medial view of left (above) and right preopercles to show interopercle in place on bone above and shallow groove to accommodate it on bone below; range in length from anteroventral to posterodorsal ends 22.3 to 54.0 mm. Upper right, opercles: upper horizontal row, left side; lower horizontal row, right side; range in greatest length 16.4 to 40.6 mm. Lower right, ventral postcleithra: upper horizontal row, left side; lower horizontal row, right side; range in greatest length 22.0 to 70.5 mm.

terior 18.5 mm; preopercle length, from posterodorsal end to estimated anterior end 55.0 mm; opercle length, from dorsal end to estimated ventral end 26.7 mm; ethmoid region width (ethmoid and vomer combined) 6.8 mm when corrected for fracture; distance between lateral edge of left pterotic and midline of cranium 22.4 mm, therefore about 45 mm greatest width of cranium when corrected for displaced right pterotic; greatest width between lateral edges of lateral ethmoids 29.8 mm when corrected for fracture; greatest width between anterolateral flanges of sphenotics at rear of orbit 37.0 mm when corrected for fracture; distance between rear edge of extreme lateral end of lateral ethmoid and front edge of anterolateral process of frontal (and sphenotic) at rear of orbit 11.5 mm on right side and 12.3 mm on left, average 11.9 mm.

To obtain an estimate of the standard length of the fossil fish represented only by the skull with a 72.5 mm cranium, measurements comparable to those above were taken on the five largest dried skeletons of *S. maculatus* available to us: 171 to 205 mm SL, which have slightly smaller crania, 49.3 to 58.8 mm, than that of *S. hyperostosus. Sphoeroides maculatus* was used in this comparison rather than *S. pachygaster* or some other species simply because of the availability of a far greater number of large specimens of *S. maculatus* either preserved in alcohol or as skeletal preparations on which we could record skull measurements than of *S. pachygaster* (several test extrapolations based on *S. pachygaster* give approximately comparable results to those based on *S. maculatus*). Three of these measurements of *S. maculatus* that are relatively long and amenable to precise measurement for the five largest dried skeletons are, as averages: length of cranium 30.3% SL; length of supracleithrum 12.7% SL; length of preopercle 23.0% SL. Using the same measurements from the fossil skull and extrapolating from those of the five specimens of *S. maculatus* of 181 mm average SL gives an estimated size for *S. hyperostosus* of 245 mm SL based on the length of the cranium, 236 mm SL based on the length of the supracleithrum, and 239 mm SL based on the length of the preopercle. We use the average figure of 240 mm SL as the best estimate of the length of the specimen represented by the holotypic skull.

Since some of the thousands of disarticulated hyperostotic bones (Fig. 3) at Lee Creek are substantially larger or smaller than those of the fossil skull, we have measured the size range of each of the four most common kinds (see Materials) to estimate the length of the fish they represent based on extrapolations from *S. maculatus*. The relative lengths of these bones are not subjected to much allometric change and we have therefore used simple extrapolations rather than regression coefficients that would have required a much more exhaustive survey of *S. maculatus*. In addition to the figure given above for the preopercle, the five dried skeletons of *S. maculatus* have an average opercle length (vertical) of 11.1% SL, subopercle length (horizontal) of 7.7% SL, and ventral postcleithrum length of 20.6% SL. Employing these figures from the 181 mm average SL specimens of *S. maculatus*, the disarticulated and hyperostotic bones that dominate Unit 3 at Lee Creek represent specimens of *S. hyperostosus* of 95 to 340 mm SL based on the 1047 ventral postcleithra, 157 to 513 mm SL based on the 734 subopercles, 81 to 246 mm SL based on the 712 preopercles, and 147 to 364 mm SL based on the 211 opercles. The fewer non-hyperostotic and disarticulated bones (Fig. 4) of *S. hyperostosus* from Lee Creek have dimensions indicating that they represent specimens within the above size ranges.

Of this estimated size range of 81 to 513 mm SL, we qualify the 513 mm SL figure based on the largest subopercle. The subopercles are the most extensively swollen of the hyperostotic bones, and, whereas most of the swelling is accommodated by mediolateral expansion, a small amount of swelling also probably involves an increase in the anteroposterior dimension of the subopercle. Therefore, we reduce the maximum size figure based on the subopercles and estimate it to be about 500 mm SL.

As an example of the enormous increase in thickness of the hyperostotic bones as seen especially in the subopercle, the largest disarticulated subopercle of *S. hyperostosus* is 39.6 mm in horizontal length and 18.4 mm in mediolateral thickness (thickness 46% of length), whereas in a somewhat smaller but slightly more swollen subopercle the length is 34.2 mm and the thickness 16.9 mm (thickness 49% of length). By contrast, the non-hyperostotic subopercles in the dried skeletons of *S. maculatus* are wafer thin (thickness 4 to 6% of length), even including the strengthening ridges along the lateral surface radiating out from the groove for articulation with the opercle. Among the disarticulated opercular bones are an oper-

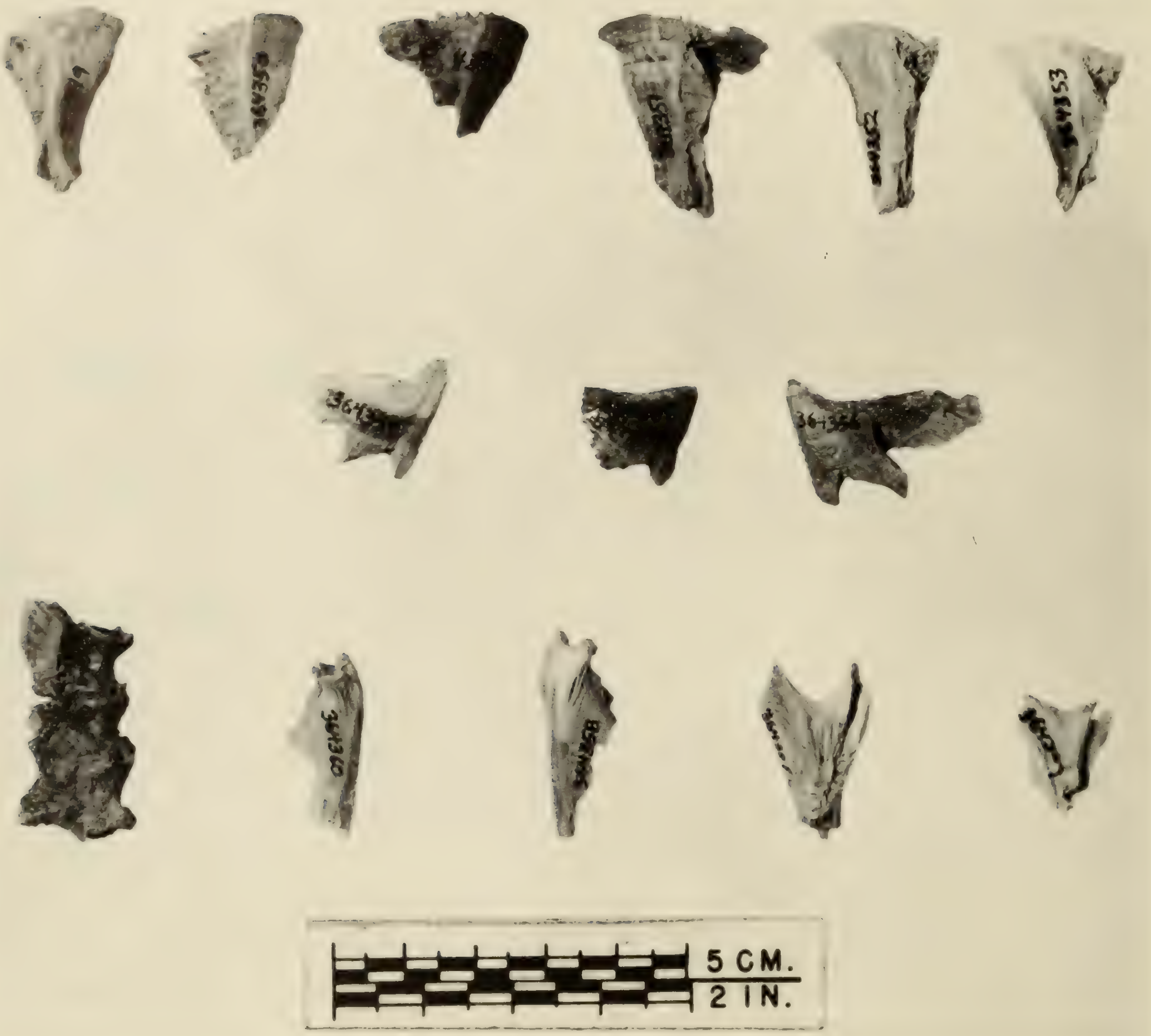

Fig. 4. *Sphoeroides hyperostosus,* a selection of non-hyperostotic bones from Lee Creek Mine. Upper row, premaxillae, those on the left from the right side and those to the right from the left side, greatest length of most intact bone (364351) 30.4 mm. Middle row, dentaries, the two on the left from the right side and that to the right from the left side, the bone numbered 437601 and the premaxilla above it of the same number removed from the holotype, greatest length of most intact bone (364356) 27.7 mm. Lower row, from left to right: second to fourth abdominal vertebrae removed from the holotype, 26.5 mm greatest length along middle of centra, lateral view; left and right palatines, greatest length 28.4 mm, obliquely lateral view; two vomers, greatest length 24.9 mm, dorsal view.

cle and subopercle that are firmly attached to one another by their hyperostosis (Fig. 5). There are no non-hyperostotic examples of tetraodontid opercular bones among the Lee Creek collections.

Comparisons

The general configuration of the bones of the holotypic fossil skull has been compared to that in the other genera of tetraodontids, as described and illustrated by Tyler (1980: 313–324, figs. 226, 227, 245, 257–261). The fossil is most similar to *Sphoeroides,* especially as seen in the proportions of the ethmoid and the configuration of the frontals where they separate the lateral ethmoids anteriorly and the sphenotics more posteriorly. The major osteological features that

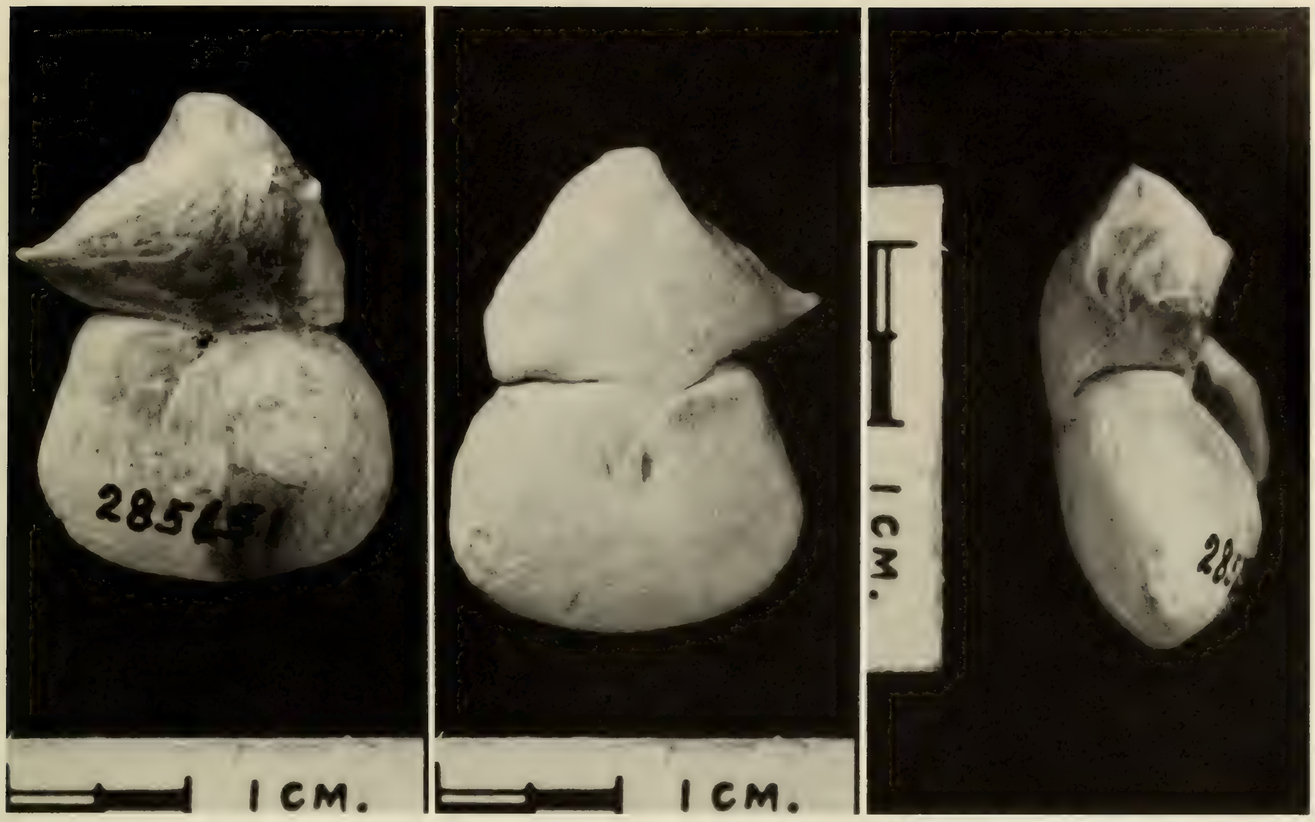

Fig. 5. *Sphoeroides hyperostosus,* USNM 285651, an opercle (above; much abraded dorsally) and subopercle from the left side held tightly together by hyperostosis; medial view to left, lateral view in middle, and posterior view to right to show the thickness of the bones; greatest vertical length of the two bones together 27.3 mm; greatest horizontal length, that of the subopercle, 19.1 mm; greatest thickness, that of the subopercle, 10.8 mm.

distinguish *Sphoeroides* from the genera most closely related to it (*Lagocephalus, Pelagocephalus, Takifugu, Torquigener* and *Amblyrhynchotes*) have been summarized by Tyler & Paxton (1979). Unfortunately, only a few of these are features that can be seen in the holotypic fossil skull, but those three that can be determined are consistent with its placement in *Sphoeroides*: there are trituration teeth in the upper jaw (at least one tooth present); there is no dorsal flange of the parasphenoid in the orbit; and there are well-developed remnants of the anterior edge of the dorsal roof of the myodome. Since the holotypic skull is closest in form to that of *Sphoeroides,* we analyze below those features that distinguish it from all of the other species of *Sphoeroides* and those that indicate its relationships within that genus.

Within *Sphoeroides* the single most important cranial character that is likely to be seen in a fossil and to be a reliable indicator of at least general relationships is the width of the interorbital. The 12 Atlantic species have been systematically redescribed and phenetically related mostly on the basis of external characters by Shipp (1974). Shipp gives data on the interorbital width for each species. These measurements were obtained by calipers externally through the skin, but they were taken with such firm pressure of the skin against the bone that Shipp's measurements are equivalent to ours made on skeletal material (R. L. Shipp, pers. comm.). For example, Shipp (1974:140) gives the range and mean of the least interorbital width for 20 specimens of *S. maculatus* of 83–217 mm SL as 5.0–7.0% SL (aver. 5.8), whereas our measurements for 29 specimens of *S. maculatus* of 75–225 mm SL are 4.6–6.6% SL (5.8), with width into cranial length figures of 4.5–5.5 times (5.0). For another species discussed below, *S. pachygaster,* Shipp (1974:138) gives the interorbital width as 6.2–12.2% SL (8.7) and especially

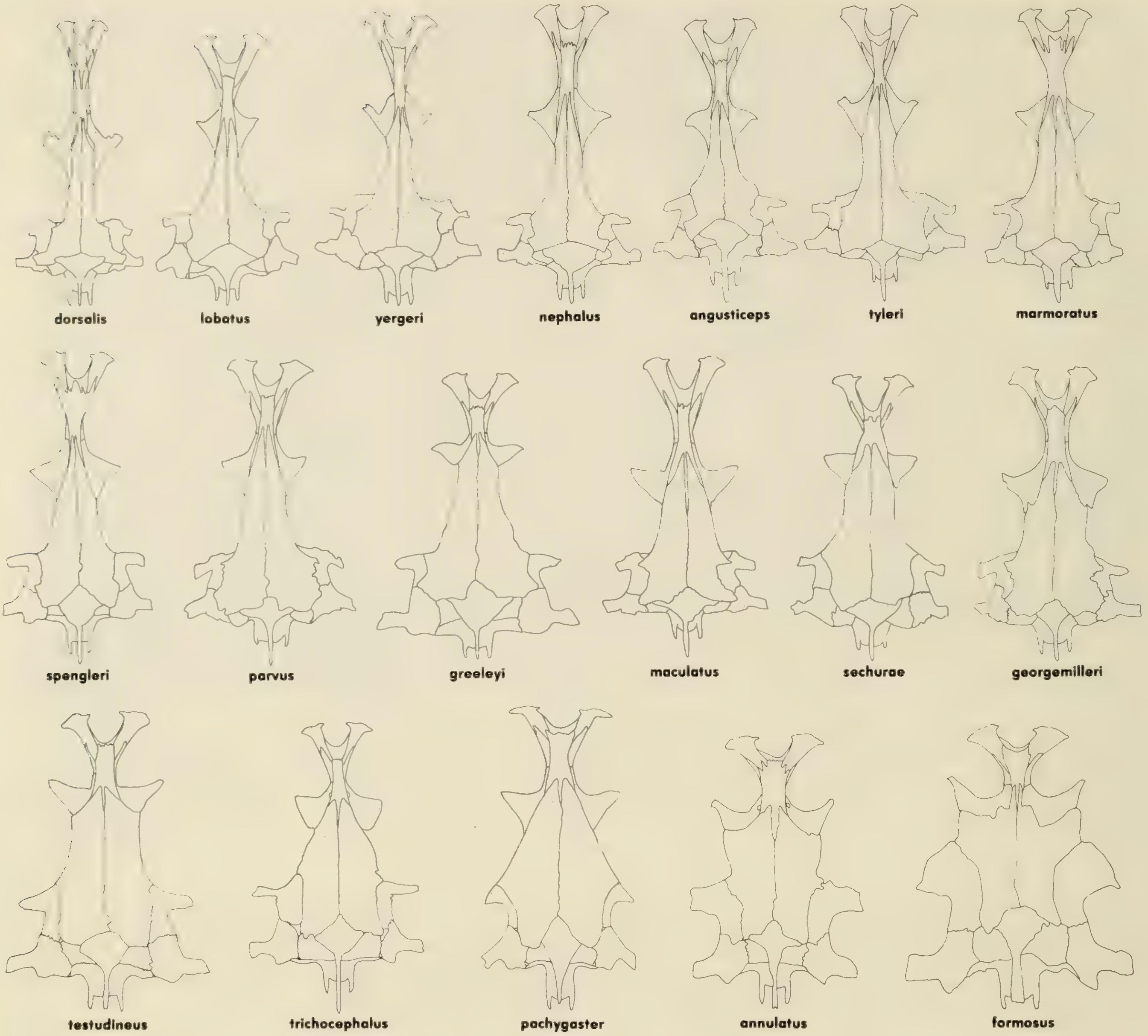

Fig. 6. Outlines of dorsal views of the skulls in the 18 extant species of *Sphoeroides,* to show the variation in interorbital width in this genus from extremely narrow to extremely broad.

variable in 20 specimens of 90–188 mm SL, with which our eight specimens agree. Tyler (1980) treated the osteology and phenetic relationships of 12 species of *Sphoeroides,* including five of the six eastern Pacific species, and illustrated dorsal views of the skull from which interorbital width can be obtained for all 12 species. For present purposes we have examined and illustrated in dorsal view the skulls of the six extant species of *Sphoeroides* not treated by Tyler, including the only species not treated by either Shipp or Tyler, *S. sechurae* from the eastern Pacific, so that the skulls of all 18 extant species may be more easily compared here (Fig. 6).

Interorbital width, expressed in this survey as the average number of times the least bony interorbital width is contained in the cranial length, is exceptionally diverse in *Sphoeroides,* more so than in any other speciose genus of tetraodontids (e.g., width is remarkably similar in all of the 23 species of *Canthigaster*). The least interorbital width in adults of the 18 extant species of *Sphoeroides* ranges from: extremely narrow (about 10.5 times in cranial length) in *lobatus, yergeri,* and *dorsalis*; to relatively narrow (6.5

to 9.0) in *angusticeps, marmoratus, nephelus,* and *tyleri*; to moderate (4.0 to 6.0) in *georgemilleri, greeleyi, maculatus, parvus, sechurae, spengleri,* and *testudineus*; to relatively broad (3.0 to 3.5) in *pachygaster* and *trichocephalus*; and to extremely broad (2.0 to 2.5) in *annulatus* and *formosus.* In the only previously described fossil species of *Sphoeroides, S. jamestyleri* Bannikov (1990) from the Miocene of the Crimea (southern Ukraine), the interorbital is relatively narrow, 7.1 times in cranial length.

We do not attempt a cladistic analysis here because we have only gross skull characters for *S. hyperostosus* and none of the numerous external body characters useful in recognizing at least phenetic groups within the Recent species of *Sphoeroides,* which have not been analyzed cladistically. However, we note that a moderate to relatively broad interorbital is generalized in tetraodontids, for that is the adult condition in most of the other genera of both of the subfamilies (tetraodontins and canthigasterins) of the Tetraodontidae and in the Triodontidae (least interorbital 2.5 times in cranial length), the most morphologically generalized family of extant tetraodontoids (triodontids being the sister group of all of the other extant families of tetraodontoids—the tetraodontids, diodontids, and molids). Moderate interorbital width also is the condition in the Triacanthodidae (4.0), the most morphologically generalized tetraodontiform family, whereas the interorbital is much broader in the Molidae (2.0) and greatly increased in width in the Diodontidae (1.0). The interorbital width is unknown in the Eocene Eoplectidae, which is the most morphologically generalized family of tetraodontoids and the sister group of all of the extant families of that group (in Tyler & Patterson 1991:878, the first author by *lapsus calami* reversed the relationship of the Eoplectidae and Triodontidae).

In *S. hyperostosus* the least interorbital width is moderate, contained 4.8 times in the cranial length (or 6.3% SL based on the extrapolated 240 mm SL). Of the seven extant species of *Sphoeroides* with a moderate interorbital, *S. hyperostosus* has a skull structure relatively similar to that of *S. parvus* and *S. maculatus,* which have interorbital widths of 5.5 and 5.0 respectively. *Sphoeroides parvus* and *S. maculatus* are believed to be very closely related within a complex of four species, the other two of which, *tyleri* and *nephelus,* have narrower interorbitals of 8.0 and 9.0 respectively (Shipp 1974:128–129). All four of these are western Atlantic species, and two of them, *maculatus* and *nephelus,* occur along the Atlantic coast of the United States. It might be expected that *S. hyperostosus* from the Pliocene of coastal North Carolina would be most closely related to one of these two, especially to *maculatus,* which has a similar interorbital width, rather than to *nephelus,* which has a narrower interorbital. We note that there is no assurance that *S. hyperostosus* was confined to the Atlantic coast of the United States and since its one locality of collection is a relatively deep water habitat it is possible that, like *S. pachygaster* discussed below, it was far more widely distributed.

These general features of similarity, including the generalized interorbital width, between the skull of *S. hyperostosus* and those of *S. maculatus* from the Carolinas and *S. parvus* from the Gulf of Mexico, cannot be used to establish how closely they might be related. However, the several unusual features of the skull (Fig. 7) that distinguish *S. hyperostosus* from the members of the complex that includes *S. maculatus* are comparable to specializations found in the deep water *S. pachygaster* of nearly circumglobal distribution, as follows.

In *S. hyperostosus* the dorsal surface of the lateral ethmoid is flat and smooth, and lacks an anteroventrally sloping surface in the anterior region. The flat anterolateral region of the upper surface of the lateral ethmoid forms a narrow shelf over the region of the olfactory apparatus. No other

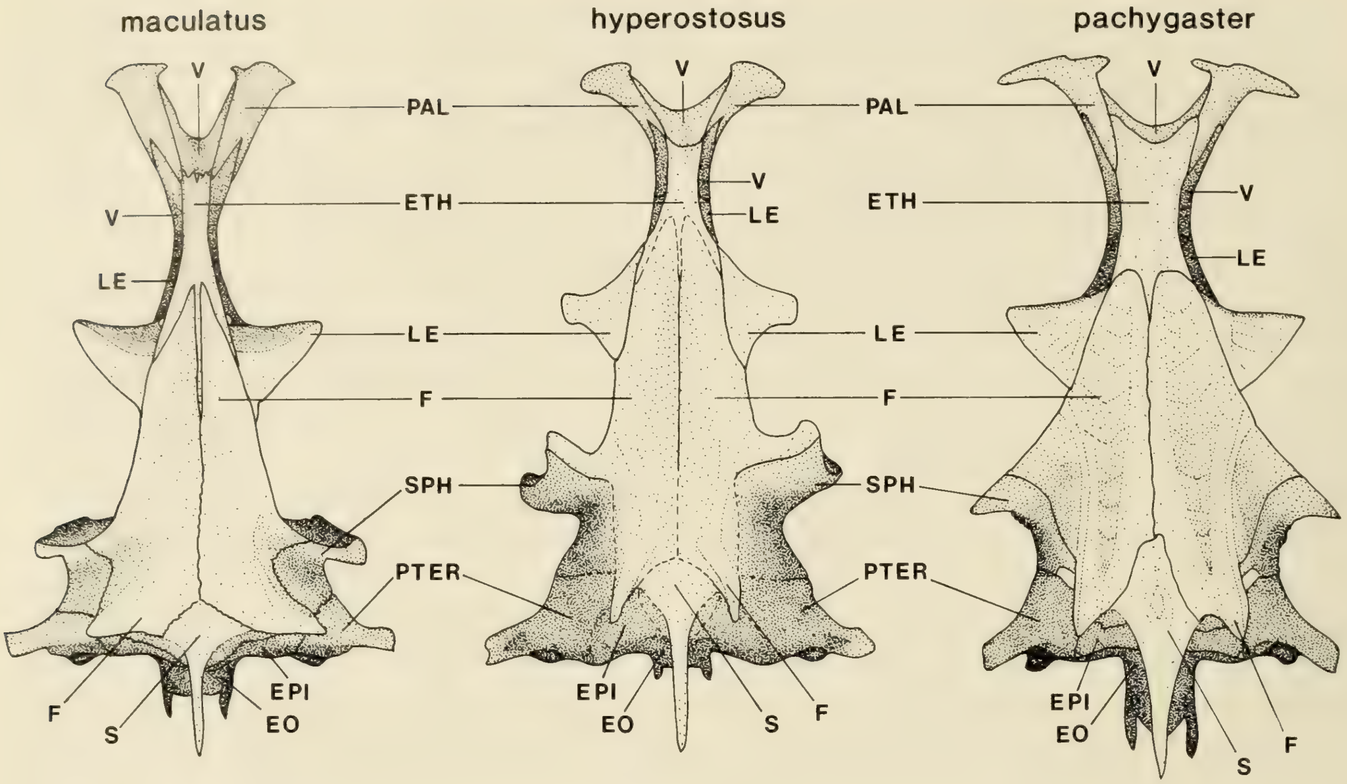

Fig. 7. Dorsal view of the skull of *Sphoeroides hyperostosus* (USNM 437601, ca. 240 mm SL) in comparison to those of *S. maculatus* (ANSP 109517, 179 mm SL) and *S. pachygaster* (ANSP 104781, 117 mm SL); the skull of *S. hyperostosus* reconstructed with correction for the distortion associated with the fracture along the left side of the frontal and ethmoid.

species of *Sphoeroides* has such a flat upper surface to the lateral ethmoid, nor a shelf over the olfactory region. Rather, all the other species of *Sphoeroides* have some degree of oblique anteroventral slope to the front edge of the lateral ethmoid (for extant species see Tyler 1980, figs. 257–262), as is also the case in the genera considered closely related to *Sphoeroides*.

However, the oblique slope is least developed in *S. pachygaster*, and in some specimens the slope is essentially absent (Fig. 7 shows the average condition of a slight oblique slope), and the anteroventral edge of the prefrontal in *S. pachygaster* does not form such a definite shelf over the olfactory region as in *S. hyperostosus*. Thus, in the shape of its lateral ethmoid, *S. hyperostosus* is most similar to *S. pachygaster* among all of the species of the genus. Nevertheless, the dorsal surface of the lateral ethmoid, and of the frontals, in *S. pachygaster* differs from all other species of *Sphoeroides* in being deeply and delicately sculptured by crests and grooves, and in being only weakly ossified, with the frontals sometimes having cartilaginous edges (Shipp 1974:127, Tyler 1980:319).

In *S. hyperostosus* the posterodorsal region of the orbit is bounded by a strong laterally and somewhat anteriorly directed process formed by the frontal (anteriorly) and sphenotic (posteroventrally). In most other species of *Sphoeroides*, including the Miocene *S. jamestyleri* and all the extant species with moderate or only somewhat wider or narrower interorbitals, only the posterior wall of the orbit is bounded by a lateral process. Moreover, when present this process is formed by the sphenotic alone, without the involvement of a strong process from the frontal at about a right angle to the rest of the bone, as in *S. hyperostosus*. In the two species of *Sphoeroides* with extremely broad interorbitals, *S. annulatus* and *S. formosus*, the sphenotic is expanded laterally and in one case (*formosus*) anteriorly as well, over the rear of the upper orbit. However, in these two species the sphenotic expansion is associated with the general broadening of the skull and differs from the condition in *S. hyperostosus* by not involving a lateral process of the frontal and not forming a strong thick process over just the posterodorsal region of the orbit.

The only configuration of the bones at the upper rear of the orbit comparable to that in *S. hyperostosus* is found in *S. pachygaster*. The frontals in *S. pachygaster* broaden posteriorly over the orbit in a relative straight line behind the lateral ethmoids and meet prominent anterolaterally directed processes from the sphenotics that roof over the posterolateral region of the orbit. While the contribution to this roofing by the frontal is not as distinctively at a right angle to the longitudinal axis of the frontal as in *S. hyperostosus*, the prominent contribution in *S. pachygaster* of an anterolaterally oriented part of the sphenotic is distinctive and similar to that in *S. hyperostosus*, more so than to any other species of *Sphoeroides* (again, excepting the special case of the sphenotic involved in the great broadening of the top of the cranium in *annulatus* and, especially, *formosus*).

The strong anterolateral frontal-sphenotic process at the rear of the orbit in *S. hyperostosus* leaves less of an open space over the eye between it and the lateral ethmoid than in any of the other species of *Sphoeroides* with a moderate interorbital width. In *S. hyperostosus* the distance between the rear edge of the extreme lateral end of the lateral ethmoid and the front of the anterolateral process of the frontal-sphenotic is about 5.0% SL (average for both sides; based on extrapolated 240 mm SL of holotype) or 78% of the interorbital width (=1.3 times into interorbital). By contrast, for example, this distance in the five largest (and therefore most comparable) specimens of *S. maculatus* examined (201–225 mm SL) averages 9.5% SL (range 8.2–10.1) or 162% of the interorbital width (=0.6 times into interorbital), and in six specimens of *S. pachygaster* (127–218 mm SL) averages 11.5% SL (range 10.8–12.4) or 138% of the interorbital width (=0.7 times into interorbital). In the fossil *S. jamestyleri*, the distance between the lateral ends of the lateral ethmoid and sphenotic is relatively great, 351% of the interorbital width (=0.3 times into interorbital) (this measurement cannot be given accurately as % SL because of distortion in the axial skeleton of the paratype, in which the skull is exposed in dorsal view and the interorbital can be measured).

In *S. hyperostosus* the frontal has a thickened ridge on its dorsal surface coursing from the rear of the orbit somewhat medially to about the anterior end of the supraoccipital, and then continuing posterolaterally around the main body of the supraoccipital to end as a short narrow posteriorly directed process over the upper end of the epiotic. In all other species of *Sphoeroides* with the exception of *S. pachygaster* the dorsal surface of the posterior region of the frontal is relatively flat and plain, although often with a deep concavity posterolaterally that is confluent with the depression between the lateral flanges of the sphenotic and pterotic. In many of these other species of *Sphoeroides*, including *S. maculatus*, the extreme posterolateral edge of the frontal protrudes out beyond the upper end of the epiotic and pterotic to form a short roof, especially laterally. In *S. pachygaster* the uniquely deeply sculptured surface of the frontal bears a ridge from the middle of the orbit that courses in a gentle curve to the lateral edge of the posterior end of the frontal, which projects posteriorly as a short but relatively broad roof over the upper surface of the epiotic. The projecting posterior end of the frontal that forms the roof in *S. hyperostosus* and *S. pachygaster* differs from that of other species of *Sphoeroides* in being directed primarily posteriorly rather than posterolaterally and in being associated with ridges running back from the orbital region, while this roof in *S. pachygaster* is larger than in all of the other species.

In addition to its weak ossification, deep sculpturing on the dorsal surface, and extensive frontal shelf over the epiotic, there are several other specializations by which the skull of *S. pachygaster* differs from that of other species of *Sphoeroides,* including the complete loss of the rudiments of the dorsal roof of the myodome, the lateral expansion of the articular facet of the palatine, and the absence of teeth on the first pharyngobranchial. By contrast, *S. hyperostosus* has especially well-developed remnants of the dorsal roof of the myodome and a palatine articular facet of moderate width (the branchial arches are unknown). In addition to its more moderate interorbital width, *S. hyperostosus* differs from *S. pachygaster* by its greater maximum size; even though *S. pachygaster* is one of the largest species of *Sphoeroides,* reaching a maximum size of 218 mm SL (USNM 42143, slightly longer than the 208 mm SL maximum size recorded by Shipp 1974:50–51), it is only about half the maximum length of *S. hyperostosus.* None of the contrasting features of *S. hyperostosus* and *S. pachygaster* can be attributed to size differences, including the hyperostosis that is the norm in *S. hyperostosus* throughout its size range of about 80 to 500 mm SL.

The extant *Sphoeroides* are all shallow water in-shore species that usually occur in depths less than 35 m, with the single exception of *S. pachygaster,* which usually is found in waters deeper than 100 m. The Pliocene *S. hyperostosus,* occurring in waters estimated to be between 50 and 80 m depth (Gibson 1967), has a depth distribution intermediate between that of *S. pachygaster* and all of the other extant species of *Sphoeroides.* The depth of the habitat of the Miocene *S. jamestyleri* has not yet been estimated but it was probably at least as deep as that of *S. pachygaster* and *S. hyperostosus* because the mesopelagic stomiiform *Vinciguerria merklini* Danilchenko is by far the most commonly preserved fish in the same Miocene deposits (Bannikov 1990:76).

Relationships

In each of the three most distinctive features of its skull *S. hyperostosus* exhibits some similarity with *S. pachygaster* alone among the 18 extant and the only other fossil species of *Sphoeroides*: (1) the lateral ethmoid with a broad upper surface without an obliquely sloping anterior edge (*hyperostosus*) or with only a slightly sloping anterior edge (*pachygaster*); (2) the posterodorsal region of the orbit roofed over by a strong anterolaterally directed process of the frontals and sphenotics (*hyperostosus*) or by a broader shelf from a lateral expansion of the frontal and an anterolateral extension of the sphenotic (*pachygaster*); and (3) the frontal with ridges from the orbital region extending onto a narrow (*hyperostosus*) to relatively broad (*pachygaster*) posteriorly directed expansion as a short shelf over the upper region of the epiotic.

Since these features do not occur in any of the other species of *Sphoeroides* or in species of other genera whose skulls are generally similar to that of *Sphoeroides* (the group of six genera to which *Sphoeroides* is allied, as characterized by Tyler & Paxton 1979), we are confident that these are specializations indicating that *S. hyperostosus* and *S. pachygaster* are each others closest relatives. The difference in the width of the interorbital in *S. hyperostosus* (6.3% SL) and *S. pachygaster* (7.0–9.7, average 8.4% SL) is not as significant as their shared specialized features. With less assurity we believe that the overall similarity of the skull of *S. hyperostosus* with that of *S. maculatus* and *S. parvus,* including the width of the interorbital, is suggestive of a relationship of *S. hyperostosus* and *S. pachygaster* with the complex of four species that includes *S. maculatus, S. parvus, S. tyleri* and *S. nephelus* as delimited by Shipp (1974). Figure 8 shows

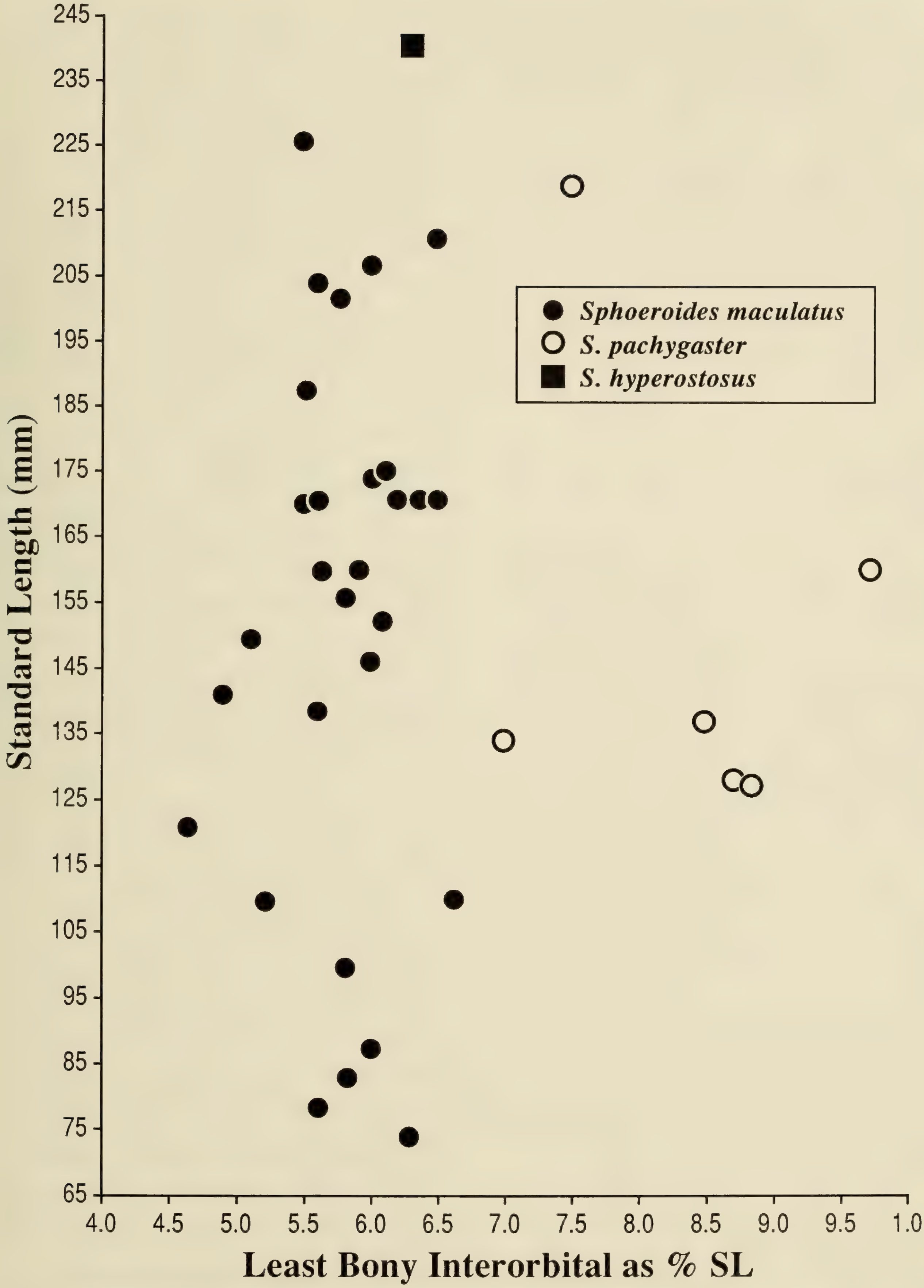

Fig. 8. Comparison of interorbital width between *Sphoeroides hyperostosus* and *S. pachygaster* and a representative (*S. maculatus*) of the species complex to which they may be most closely related.

the relative width of the interorbital, and its constancy with increasing specimen size in adults, of *S. hyperostosus, S. pachygaster,* and *S. maculatus.*

Hyperostosis in the Tetraodontidae

Hyperostosis has been found previously in only two genera of tetraodontids: in four species of *Lagocephalus* and in the monotypic *Xenopterus.* Abe (1960:406) and Abe et al. (1984:2) reported that the neural and haemal spines of some of the vertebrae in the caudal peduncle in *L. lunaris* and *L. spadiceus* are hyperostotic, whereas the lateral ethmoid, preopercle, and ventral postcleithrum are hyperostotic in *L. lunaris* but not in *L. spadiceus.* Abe & Tabeta (1983:5) also found that the neural and haemal spines of two of the vertebrae of the caudal peduncle (usually those of the 14th and 15th, but sometimes of the 13th and 16th vertebrae), the anterior end of the cranium (presumably ethmoid region) and the postcleithrum (dorsal or ventral not specified) of *L. gloveri* are hyperostotic in the majority of preserved specimens (205–320 mm SL) but apparently not in smaller specimens. Tyler (1980:268, 273, 323) reported that the ethmoid and the haemal spines of the 6th and 7th caudal vertebrae of *L. laevigatus* are hyperostotic in large specimens, but that the neural spines in this region of the caudal peduncle are not hyperostotic. We report here that in the single large specimen of *L. inermis* examined for this work (see Materials) the ethmoid and the haemal spines of the 6th, 7th, and 8th caudal vertebrae and the neural spine of the 7th caudal vertebra are hyperostotic.

Tyler (1980:340) reported that the frontals and the neural and haemal spines of the penultimate vertebra are hyperostotic in *Xenopterus naritus. Xenopterus* is one of the most specialized tetraodontids, with long-based dorsal and anal fins, an increased number of vertebrae and an open sac nasal apparatus. It is not considered to be closely related to *Lagocephalus,* and the development of hyperostosis in *Xenopterus* and *Lagocephalus* must be independent.

We have examined hundreds of radiographs and cleared and stained specimens of the majority of extant species of tetraodontids in conjunction with previous research on the group (skeletal materials as listed in Tyler 1980:395–397; and the radiographs that were used to obtain most of the vertebral data in table 2 of that work) and have found hyperostosis only in those species of *Lagocephalus* and *Xenopterus* cited above. For the present study, we have radiographed a series of the largest specimens of *S. pachygaster* and *S. maculatus* available to us (see Materials) to explore the possibility that only especially large individuals of those species may develop hyperostosis, but none of these large specimens was found to exhibit this condition.

Hyperostosis is found almost exclusively among marine fishes. In the only well-documented example of hyperostosis in a nonmarine fish, that of the Miocene cyprinodontid *Aphanius crassicaudus* (Agassiz), it has been postulated by Gaudant (1978, 1979), Meunier & Gaudant (1987), and Landini & Sorbini (1989) that the development of this hyperostotic condition is caused by fluctuations in the salt content of evaporating shallow bodies of water over gypsum (hydrous calcium sulfate) beds that become temporarily cut off from the sea. While the link between hyperostosis and extreme environmental conditions is well substantiated in that euryhaline species, the habitat of *S. hyperostosus* was normal coastal marine waters of about 50 to 80 m depth, and nothing associated with its habitat could reasonably be proposed as an abnormal condition that might in some way cause hyperostosis.

Hyperostosis is not known to occur to any unusual degree in the specimens of fishes from Lee Creek; the fish species from that formation that exhibit hyperostosis are the same as those that exhibit it in extant groups, i.e., some ephippiids, carangids, gadids, etc. (based on manuscript by R. Purdy et al. describing the Lee Creek ichthyofauna). This, plus the fact that hyperostosis occurs in a wide size range of specimens (presumably over many generations and thousands of years of deposits) of *S. hyperostosus* and that without exception all of the thousands of disarticulated opercles, subopercles, preopercles, and ventral postcleithra that remain of the species are hyperostotic, leads to the reasonable conclusion that hyperostosis in *S. hyperostosus* is normal.

Acknowledgments

We are especially indebted to Craig Healy of Lexington, South Carolina, for his extraordinary and highly perceptive collecting efforts at Lee Creek Mine which resulted in the recovery of the first intact skull of a pufferfish and therein the solution to the mystery of the origin of the thousands of disarticulated hyperostotic bones from that formation. His generosity in donating this skull to the Smithsonian Institution is deeply appreciated.

We are grateful to Robert L. Shipp, University of South Alabama, Alexandre F. Bannikov, Paleontological Institute, Moscow, and Keiichi Matsuura, National Science Museum, Tokyo, for their comments on the manuscript, and to Richard P. Vari and G. David Johnson, National Museum of Natural History, for permission to make superficial dissections on numerous specimens of *Sphoeroides* in the collections of the Division of Fishes, while Lynne R. Parenti of that Division discussed with us the implications of hyperostosis in *Aphanius* and Susan L. Jewett, Sandra I. Raredon, and William F. Hoffman made many of the radiographs for this study. Bruce B. Collette and Janet Nestlerode, National Marine Fisheries Service Systematics Laboratory, and Vic Krantz, National Museum of Natural History, generously provided the photographs herein. We greatly appreciate the cooperation of William F. Smith-Vaniz, Eugenia B. Böhlke, and William G. Saul, all of the Academy of Natural Sciences of Philadelphia, for the loan of specimens and radiographs.

We have benefited from discussions of the systematic implications of hyperostosis with William F. Smith-Vaniz and G. David Johnson and value both their informative advice and helpful review of the manuscript. The manuscript was much improved by the preacceptance reviews of Lynn R. Parenti and R. D. Mooi, USNM.

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PHYLLOPHORUS (*URODEMELLA*) *ARENICOLA*, A NEW SUBLITTORAL SEA CUCUMBER FROM THE SOUTHEASTERN UNITED STATES (ECHINODERMATA: HOLOTHUROIDEA)

David L. Pawson and John E. Miller

Abstract.—*Phyllophorus* (*Urodemella*) *arenicola* new species is described. It is an offshore species living in depths of 6–158 meters off Georgia and eastern Florida, and it has been confused with the more widely distributed *P.* (*U.*) *occidentalis* (Ludwig 1875), known from depths of only 2 meters or less.

In the course of a monographic revision of the western Atlantic holothurians, one of us (JEM) noted that the offshore species described below is new, and that Miller & Pawson (1984) had confused this distinctive species with *P.* (*U.*) *occidentalis* (Ludwig 1875), which is known from Florida, Puerto Rico, Antigua, Barbados, Grenada, Aruba, Trinidad, Surinam and Brazil, in a depth of 0–2 m (Deichmann 1930, 1954). The specimen illustrated in fig. 27 on p. 36 of Miller & Pawson (1984) is *P.* (*U.*) *arenicola,* but the body wall ossicles (tables) illustrated in fig. 28 on p. 37 are those of *P.* (*U.*) *occidentalis.*

We are grateful to Paula Mikkelsen (Harbor Branch Oceanographic Institution), Gordon Hendler (Los Angeles County Museum), Hugh Reichardt and Woody Lee (Smithsonian Marine Station) for collaborating in SCUBA diving expeditions, and to Julie Piraino (Smithsonian Marine Station) for taking the Scanning Electron Micrographs.

Type specimens and other material are deposited in the National Museum of Natural History, Smithsonian Institution (USNM) or the Harbor Branch Oceanographic Museum, Fort Pierce, Florida (HBOM). This is Contribution No. 298 from the Smithsonian Marine Station at Link Port, and No. 900 from the Harbor Branch Oceanographic Institution.

Order Dendrochirotida Grube, 1840
Family Phyllophoridae Östergren, 1907
(emend. Pawson & Fell, 1965)

Diagnosis.—Body not enclosed by a test of conspicuous ossicles; ossicles in body wall small, inconspicuous. Calcareous ring complex, with paired or unpaired posterior processes; processes composed of a mosaic of minute pieces. (From Pawson & Fell 1965.)

Phyllophorus Grube, 1840
Phyllophorus (*Urodemella*) Deichmann, 1944

Diagnosis.—Dendrochirote holothurians with 20 tentacles in two rings (15 + 5). Calcareous ring with short projections, composed of a few pieces. Feet in large animals regularly scattered over the body. Calcareous bodies reduced towers or thorny plates derived from towers. (From Heding & Panning 1954.)

Type species.—*Phyllophorus holothurioides* Ludwig, 1875.

Remarks: In their revision of the classification of the Order Dendrochirotida, Pawson & Fell (1965) attempted to delineate families on the basis of a combination of characters of the ossicles in the bodywall and the calcareous ring. The Family Phyllophoridae in the broad sense was intended to contain only dendrochirotes in which the posterior projections of the calcareous rings are composed of numerous small pieces. Not all members of the subgenus *Urodemella* conform to this diagnosis. The western Atlantic species *P.* (*U.*) *occidentalis* (Ludwig) has a calcareous ring in which the posterior projections on the radial pieces may appear to be solid, or they may be "composed of small calcareous plates" (Ludwig 1875:119). The interradial pieces may carry "posterior accessory plates" (Deichmann 1930:149) or these plates may not be separated from the interradial pieces in certain parts of the ring, according to Deichmann. In the new species described below, the ring seems to lack accessory plates. Despite the apparent variation in the structure of the ring, the ossicles in this group are distinctive, and diagnostic.

In their diagnosis of the subgenus *Phyllophorus* (*Urodemella*), Heding & Panning (1954) noted (p. 161) that the tentacles are arranged in two rings, the outer ring with 15 tentacles and the inner ring with 5. However, in their description of *P.* (*U.*) *occidentalis,* they noted a 10 + 10 tentacle arrangement; a similar plan exists in the new species described here. Details of tentacle arrangement are apparently not reliable characters at the subgenus level in this group.

Phyllophorus (*Urodemella*) *arenicola,* new species

Figs. 1–4

Phyllophorus (*Urodemella*) *occidentalis.*—Miller & Pawson, 1984, p. 36, figs. 27, 28. (Not *Phyllophorus* (*Urodemella*) *occidentalis* Ludwig, 1875.)

Diagnosis.—Tentacles 20 in 2 rings, 5 large pairs in outer ring alternating with 5 small pairs in inner ring. Body wall ossicles square tables averaging 66 μm in length, commonly with 5 or 8 perforations, of which 2 are larger than others; spire reduced to form 4 vertical projections. Introvert and tentacles with tables and rosettes.

Type material.—Holotype (USNM E42486) and six paratypes (USNM E42487, 6 specimens) Station RF-19-88, 24 May 1988, Capron Shoal, off Hutchinson Island, St. Lucie County, Florida, 6–12 m, collected J. E. Miller and P. Mikkelsen. Six paratypes (HBOM 071:00580), Capron Shoal, off Hutchinson Island, St. Lucie County, Florida,25 Sep 1991, 27°26.859′N, 80°11.670′W, 13.8 m, collected P. Mikkelsen and W. Lee.

Additional material (abbreviated data).—USNM E19577, off Georgia, 30°57′N, 79°58′W, 158 m; USNM E19706, off Florida, 29°28′N, 80°57′W, 20 m; USNM E19709, off Florida, 29°28′N, 80°57′W, 20 m; USNM E19710, off Florida 29°28′N, 80°57′W, 20 m; HBOM 071:00353, off Florida 28°00′N, 80°12′W, 27.4 m; HBOM 071:00354, off Florida, 30°20′N, 80°14′W to 30°19′N, 80°14′W, 64–65.9 m; HBOM 071:00368, off Florida, 27°40.1′N, 80°13.5′W, 18.3 m.

Description.—Total length of live individuals may exceed 30 cm; contracted animals usually less than 10 cm long. Body more or less cylindrical, slightly U-shaped in life (Fig. 1), tapering gently towards anterior and posterior ends. Body wall thin, soft to touch, becoming firmer and thicker in contracted specimens. Color in life uniform to variegated light reddish brown. Tube feet small, soft, scattered over most of body, with tendency to form double rows in radii. At introvert feet tend to be restricted to radii, in double rows; at extreme posterior end of body, feet also restricted to radii. Tentacles 20, outer ring of 5 large pairs alternating with inner ring of five small pairs. In partially contracted paratype 115 mm long, 5 pairs of large tentacles are 7–10 mm long, 5 pairs of small tentacles are 1–2 mm long.

In 120-mm long paratype (USNM E42487) 2 Polian vesicles arise from ventral side of water-vascular ring. Intestine long, describing large loop. Respiratory trees very extensive, white-transparent, occupying most of body cavity. Gonad a large tuft of sparsely branched tubules approximately 1 cm long, arising from elongate (20 mm long) rachis near mid-dorsal body wall.

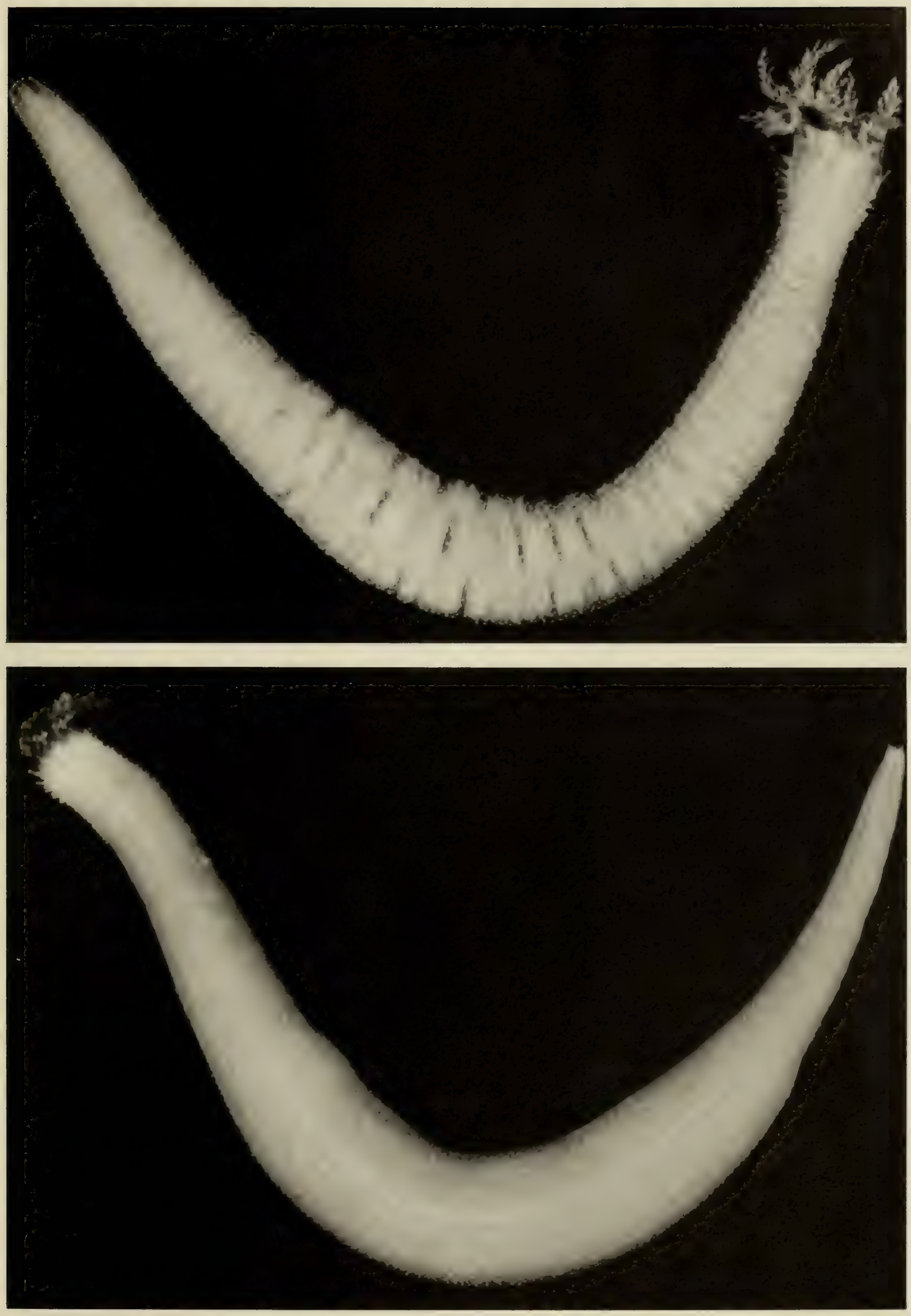

Fig. 1. *Phyllophorus* (*Urodemella*) *arenicola,* new species. Lateral views of 2 live animals. A, Upper, total length 200 mm; B, Lower, total length 220 mm.

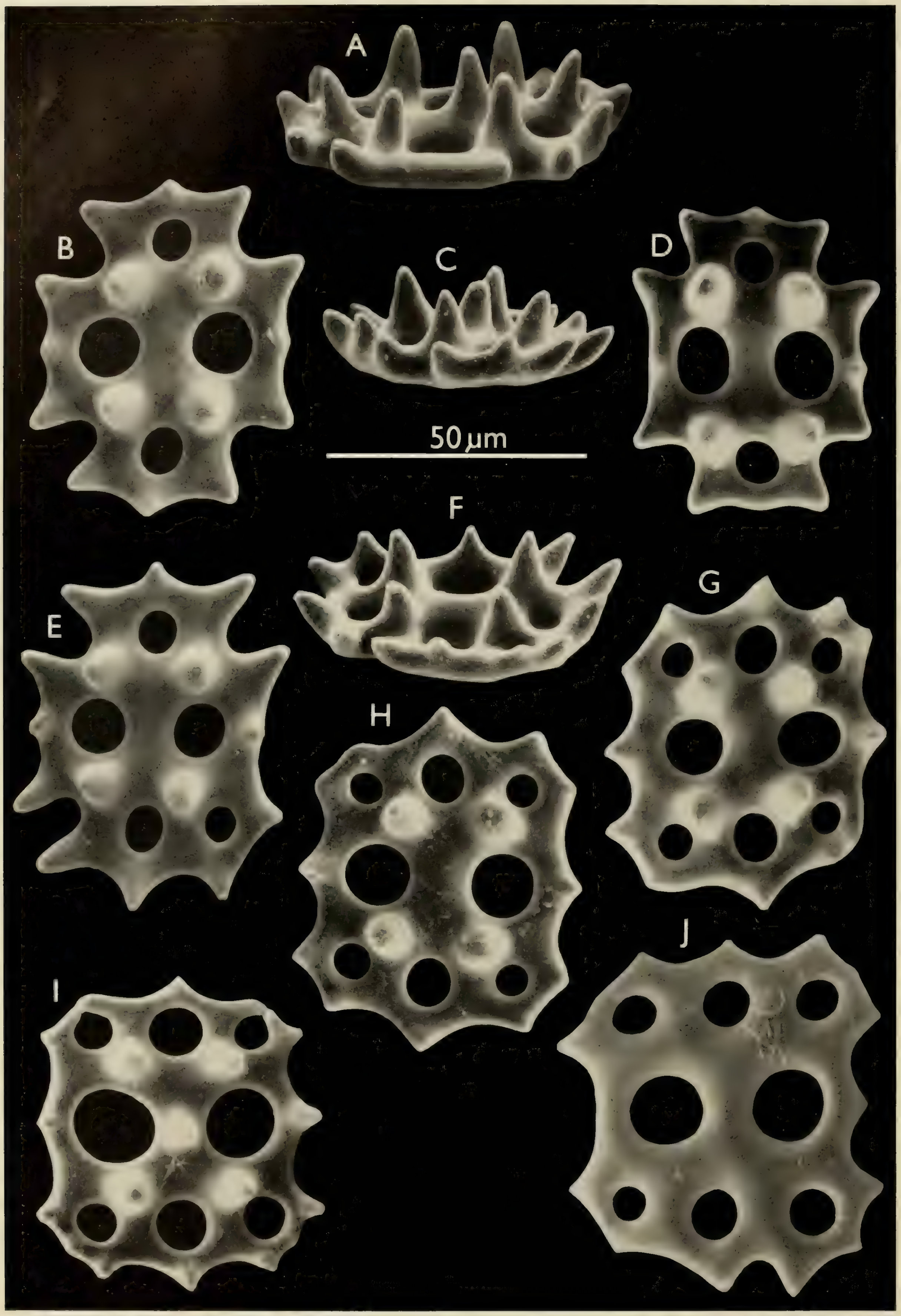

Fig. 2. *Phyllophorus* (*Urodemella*) *arenicola,* new species. Scanning electron micrographs of dermal ossicles; tables from mid-body. A, F—oblique view; B, D, E, G, H, I—outer view; C—lateral view; J—inner view.

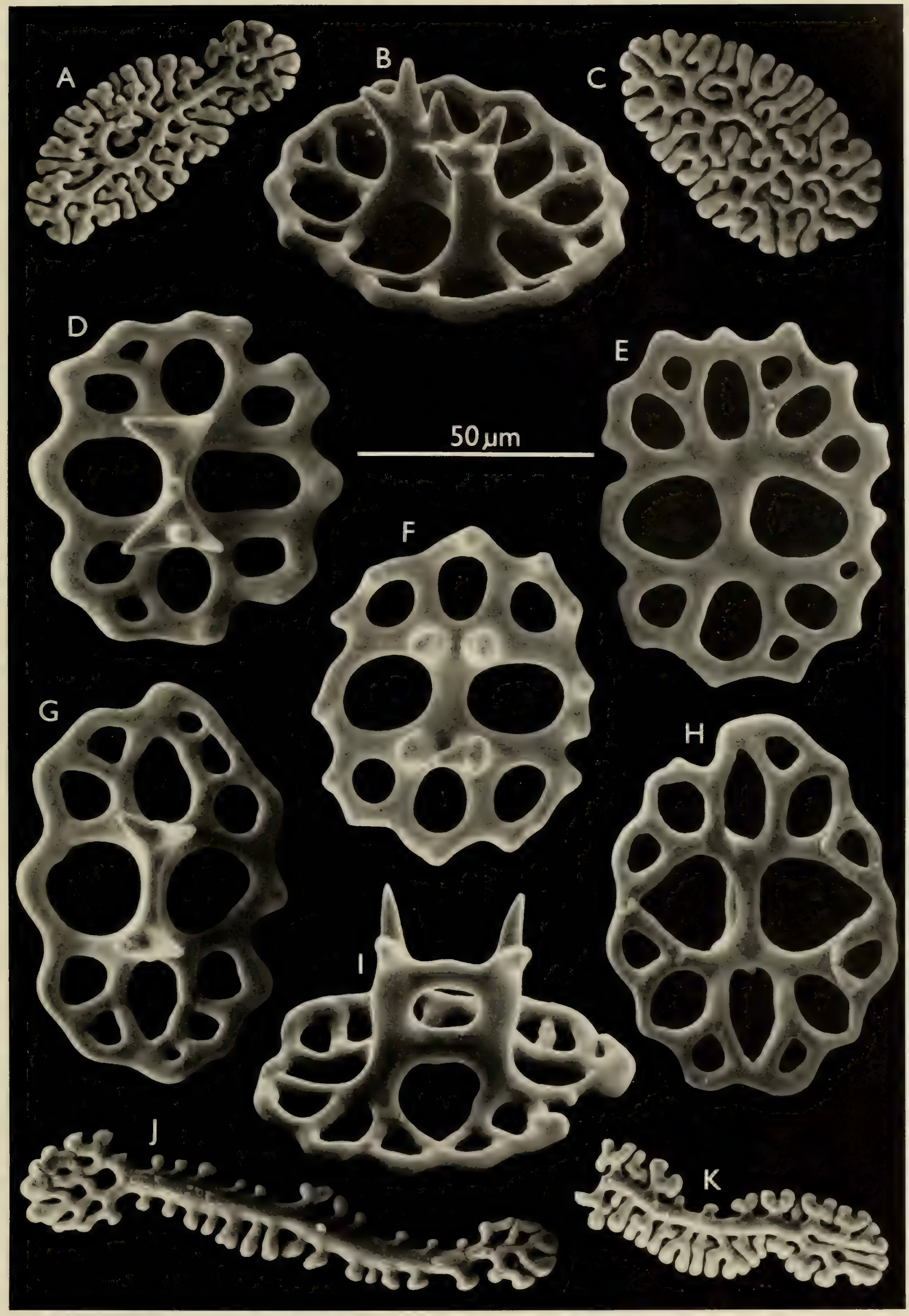

Fig. 3. *Phyllophorus* (*Urodemella*) *arenicola,* new species. Scanning electron micrographs of dermal ossicles; tables and rosettes from introvert (A–F), and from tentacles (G–K). A, C, rosettes from introvert; B, D, E, F—tables from introvert in oblique, outer, inner, and outer views respectively. G, H, I—tables from tentacles in outer, inner, and oblique views respectively. J, K—rosettes from tentacles.

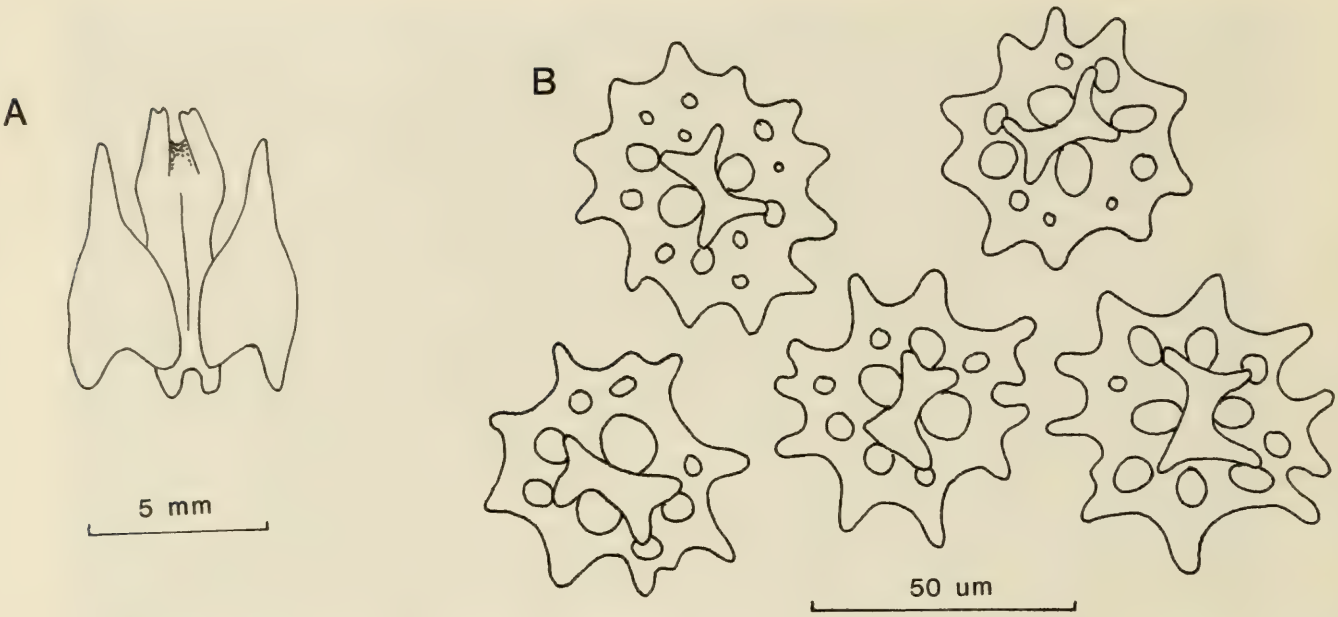

Fig. 4. *Phyllophorus* (*Urodemella*) *arenicola*, new species. A, radial and interradial pieces of calcareous ring from specimen of 90 mm total length. *P.* (*U.*) *occidentalis* (Ludwig). B, tables from body wall.

Radial pieces of calcareous ring (Fig. 4A) approximately rectangular, with deep frontal notch and 2 short posterior projections. Distinct ridge lies on long axis of outer surfaces of each radial piece. Interradials approximately oval, with sharp anterior projection and broad, shallow posterior notch. No evidence of mosaic construction of posterior projections of radial or interradial pieces.

Ossicles in body wall exclusively squarish tables (Fig. 2) with scalloped margins and 4 or more perforations; commonly 8 perforations present. In most cases 2 perforations slightly larger than others. Spire reduced to form 4 discrete bluntly pointed vertical projections. Marginal projections extend laterally and also vertically. In oblique or lateral view projections and spire pillars similar, conspicuous. Inner surface of tables (Fig. 2J) smooth. The tables are 61–74 μm long, average length 66 μm (*SD* 2.85). In introvert ossicles in form of tables (Fig. 3B, D–F) and rosettes (Fig. 3A, C). Tables slightly larger than body wall tables, usually with 8 or more perforations, of which 2 tend to be largest. Marginal projections less conspicuous than in body wall tables. Spire may be slightly better developed (Fig. 3B), or similar to spires in body wall (Fig. 3F). Inner surface of these tables (Fig. 3E) smooth. Rosettes in introvert (Fig. 3A, C) average 67 μm in length, flattened, complex, with numerous branches. Tentacles contain tables (Fig. 3G–I) and rosettes (Fig. 3J–K). Tentacle tables similar in general features to those from introvert, except that spire is usually better developed, with 2 cross-pieces (Fig. 3I). Tentacle rosettes simpler, more elongate (exceeding 120 μm in length) than introvert rosettes.

Biology.—When collected by dredging or trawling, this animal frequently is in two pieces, because the anterior end, comprising the introvert, tentacles, calcareous ring and associated structures, is commonly autotomized. At the Capron Shoal locality (the type locality), individuals live buried in an unconsolidated sand and shell hash bottom, with only their feeding tentacles extended into the water. In areas where there are ripple marks, individuals were found in the ridges, and were uncovered by pushing the tops of the ridges to one side with the hand (W. Lee & P. Mikkelsen, pers. comm.). This species can rapidly retract its tentacles and introvert to a depth of approximately 10 cm below the substrate surface.

Paratypes (HBOM 071:00580) collected in September 1991 were maintained alive in clean seawater in the laboratory for three days, and their feces collected and analysed. Feces consisted of unidentifiable flocculent material, and it seems likely that this species is a true suspension feeder, capturing organic material with its richly branched tentacles. Whether in total darkness or in lighted conditions, live animals almost never extended their tentacles, even when seawater with suspended organic particles was introduced into the holding tank.

Etymology.—The species name is a noun in apposition, derived from Latin *arena*—sand, in reference to the preferred habitat of this species.

Distribution.—Recorded from off Georgia and eastern Florida in depths of 6–158 meters. *P.* (*U.*) *arenicola* appears to be a strictly offshore species.

Remarks.—This species shares some characters with *P.* (*U.*) *occidentalis* (Ludwig). The general appearance of the body and arrangement of the tentacles is similar in both species, although they differ in color, *P.* (*U.*) *occidentalis* being light to dark brown to yellow, while *P.* (*U.*) *arenicola* always seems to be light reddish brown. The body wall tables of *P.* (*U.*) *occidentalis* (Fig. 4B) are smaller, with a size range of 49–63 μm and a mean length of 55 μm (*SD* 3.38), and the four pillars of the spire are joined together near the base. The radial pieces of the calcareous ring in *P.* (*U.*) *occidentalis* have a flat or concave outer surface—there is no trace of a longitudinal ridge.

The other species in this subgenus are known from the Indo-Pacific, and differ in numerous details from both *occidentalis* and *arenicola* (Heding & Panning 1954).

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THE IMMATURE STAGES OF *ATHERIGONA ORIENTALIS* SCHINER (DIPTERA: MUSCIDAE)

Márcia Souto Couri and Paulo Francisco de Araújo

Abstract.—The egg, three larval instars, and puparium of *Atherigona orientalis* Schiner are described. This is the first description of the first and second larval instars of this species.

Atherigona orientalis Schiner, 1868 is widespread in the warmer regions of the world. It is the only species of *Atherigona* known from South America and probably spread there through human commerce. Adults commonly breed in carrion and decaying plant matter, more rarely in feces. Eggs are laid singly and usually inserted in the soft parts of rotting substances, with only the tip of the micropylar end visible (Bohart & Gressitt 1951, Skidmore 1985). Larvae are saprophagous and may also feed on dead or moribund larvae living in the stem. In the latter case, they are scavengers or predators and not parasites (Pont 1972). Pupariation occurs inside the fibrous host material with only the anterior end of the puparium exposed. According to Bohart & Gressitt (1951), *A. orientalis* is an important carrier of fecal and other filth-borne pathogens in Guam. This species infests crops only after a primary infestation has taken place (Pont 1972). Further information on the biology can be found in Rao (1924), Bohart & Gressitt (1951), Pont (1972), and Skidmore (1985).

The morphology of some immature stages (egg, third-instar larva, and puparium) has been described and illustrated by some authors (e.g., Bohart & Gressitt 1951; Skidmore 1985), but the first and second larval instars have never been described (Skidmore 1985). We take this opportunity to describe the first and second instar larvae as well as redescribe the other immature stages so that all can be found in one place.

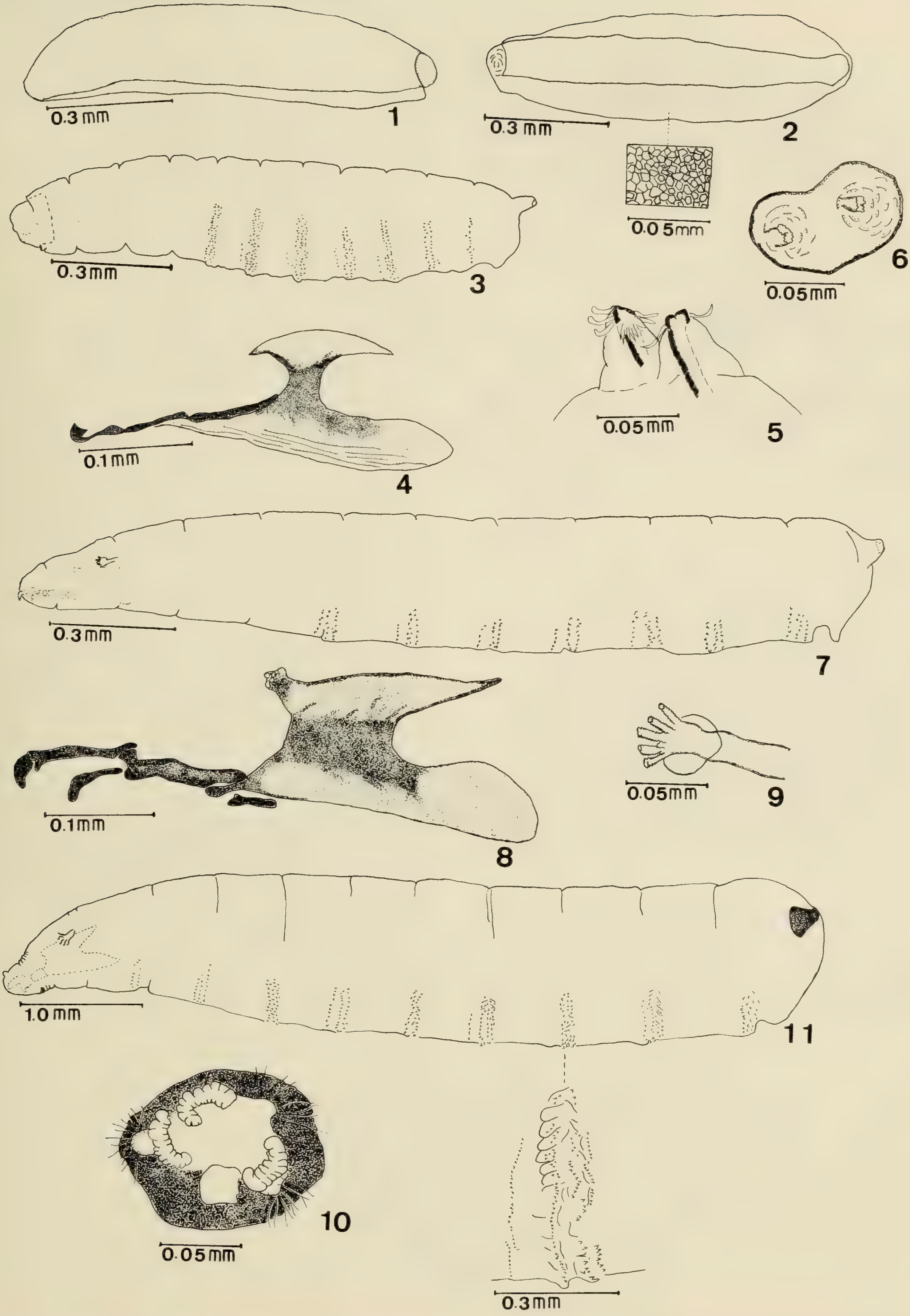
Methods.—Adults of *A. orientalis* were collected in Rio de Janeiro (Horto Botânico, Quinta da Boa Vista, São Cristóvão), Brazil, in 1991 by attracting them to fish bait. A colony was developed inside a glass container in the laboratory. Females oviposited and resulting larvae developed on a small quantity of fruit (banana). After having been cleared in a solution of potassium hydroxide, larvae were studied with a Wild M20 optical microscope.

Description of the Immature Stages of *A. orientalis*

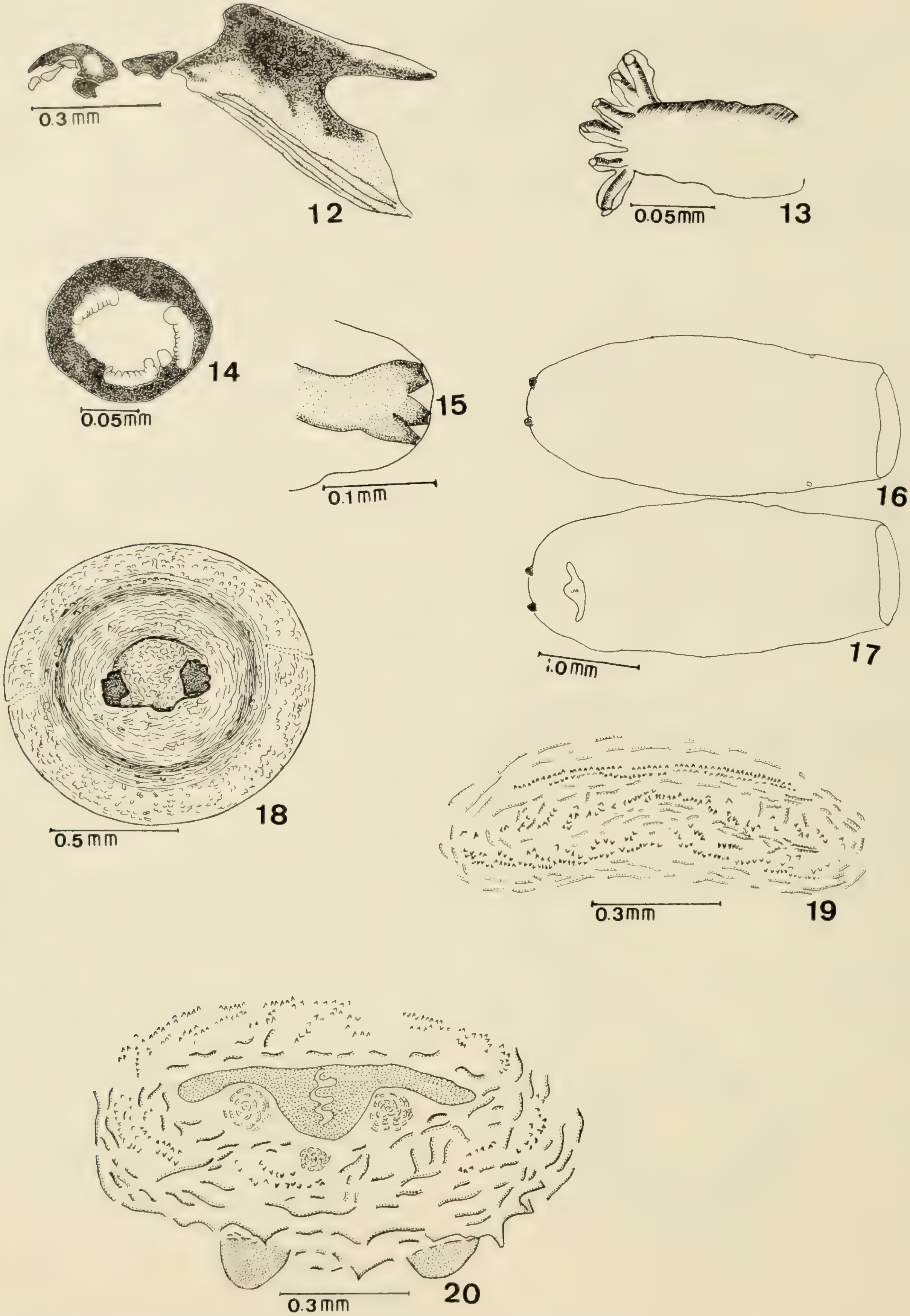
Egg (Figs. 1–2).—Length 1.0 mm. Color white. Dorsal surface ornamented with polygonal pattern. The extremities have narrow, centrolateral projections. These are better seen in profile (Fig. 2). See also Bohart & Gressitt (1951).

First-instar larva (Figs. 3–6).—Anterior spiracles absent. Second to eighth abdominal segments with irregular ventral rows of spines (Fig. 3). Posterior spiracles situated on stalks, with 2 elongate-ovoid slits and are slightly constricted in middle (Figs. 5–6); perispiracular filaments narrow. Cephalopharyngeal skeleton with dorsal horn pointed anteriorly and posteriorly, the pharyngeal constriction narrow, and ventral horn about 1.5 times longer than dorsal one; mouth hooks curved, their extremities pointed (Fig. 4).

Second-instar larva (Figs. 7–10).—Length 2.2–2.5 mm. Anterior spiracle delicate, with about five, finger-shaped projections (Fig. 9). Abdominal segments with spines as in



Figs. 1–11. *Atherigona orientalis*: 1, Egg, dorsal view; 2, Same, lateral view; 3, First-instar larva, lateral view; 4, Cephalopharyngeal skeleton, lateral view; 5, Posterior spiracle of first-instar larva, dorsoblique view; 6, Same, posterior view; 7, Second-instar larva, lateral view; 8, Cephalopharyngeal skeleton, lateral view; 9, Anterior spiracle of second-instar larva, lateral view; 10, Posterior spiracle of second-instar larva, posterior view; 11, Third-instar larva, lateral view.



Figs. 12–20. *Atherigona orientalis*: 12, Cephalopharyngeal skeleton of third-instar larva, lateral view; 13, Anterior spiracle of third-instar larva, lateral view; 14, Posterior spiracle of third-instar larva, posterior view; 15, Same, lateral view; 16, Puparium (without anterior segment), dorsal view; 17, Same, ventral view; 18, Anterior segment of puparium, dorsal view; 19, Same, dorsal view; 20, Posterior segment of puparium, ventral view.

first-instar larva. Posterior spiracles more sclerotized, the 3 spiracular slits "C" shaped (Fig. 10). Cephalopharyngeal skeleton (Fig. 8) with various parts more robust than in first-instar larva; mouth hooks curved.

Third-instar larva (Figs. 11–15).—Length 4.0–6.5 mm. Anterior spiracle with five to seven projections (Fig. 13). Thoracic and abdominal segments with rows of small spines. Posterior spiracular stalks black, the spiracles with three slits similar to those of second-instar larva (Figs. 14–15). Cephalopharyngeal skeleton with sclerites much shorter than in other instars (Fig. 12). See also Skidmore (1985).

Puparium (Figs. 16–20).—Length 3.5–4.0 mm. Segments with rows of spines, more numerous on ventral surface. Anterior abdominal segment ornamented dorsally as in Fig. 18, posterior abdominal segment ornamented dorsally as in Fig. 19. Perianal region with sinuous longitudinal opening and short spines, subanal papillae twice the diameter of the postanal papilla (Fig. 18).

Remarks.—We observed a longer life cycle than has been reported in the literature. Our colony, reared in the laboratory with a median temperature of 28°C and relative humidity of 63%, took 23.5 to 30.0 days from freshly laid egg to eclosion of the adult. The breakdown in the times of the various stages is as follows: egg, 1.0 day; first-instar larva, 0.5–1.0 day; second-instar larva, 1.0–2.0 days; third-instar larva, 9.0–11.0 days; puparium, 12.0–15.0 days. In a review of the literature, Skidmore (1985) reported a range of 11.5 days and Rao (1924 *in* Skidmore 1985) 15.5 days in the cycle from egg through pupariation.

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STUDIES OF NEOTROPICAL CADDISFLIES, XLIX: THE TAXONOMY AND RELATIONSHIP OF THE GENUS *EOSERICOSTOMA*, WITH DESCRIPTIONS OF THE IMMATURE STAGES (TRICHOPTERA: HELICOPHIDAE)

Oliver S. Flint, Jr.

Abstract.—The larvae, pupae, and cases of *Eosericostoma inaequispina* Schmid, type species of the genus, are described for the first time. Generic diagnoses are presented for the adults, larvae, pupae, and cases. The males and females of the two included species are illustrated and their known distributions plotted; distinguishing characters for the immature stages could not be found. The genus is compared with the other three genera in the family, *Helicopha, Alloecella* (both from Australia and Tasmania) and *Zelolessica* (New Zealand). Although data on the immature stages of the Australasian genera are incomplete at this time, substantial agreement is found between all four genera in most characteristics. *Eosericostoma* is considered to be a true member of the Helicophidae and represents another Trans-Antarctic element in the Chilean fauna.

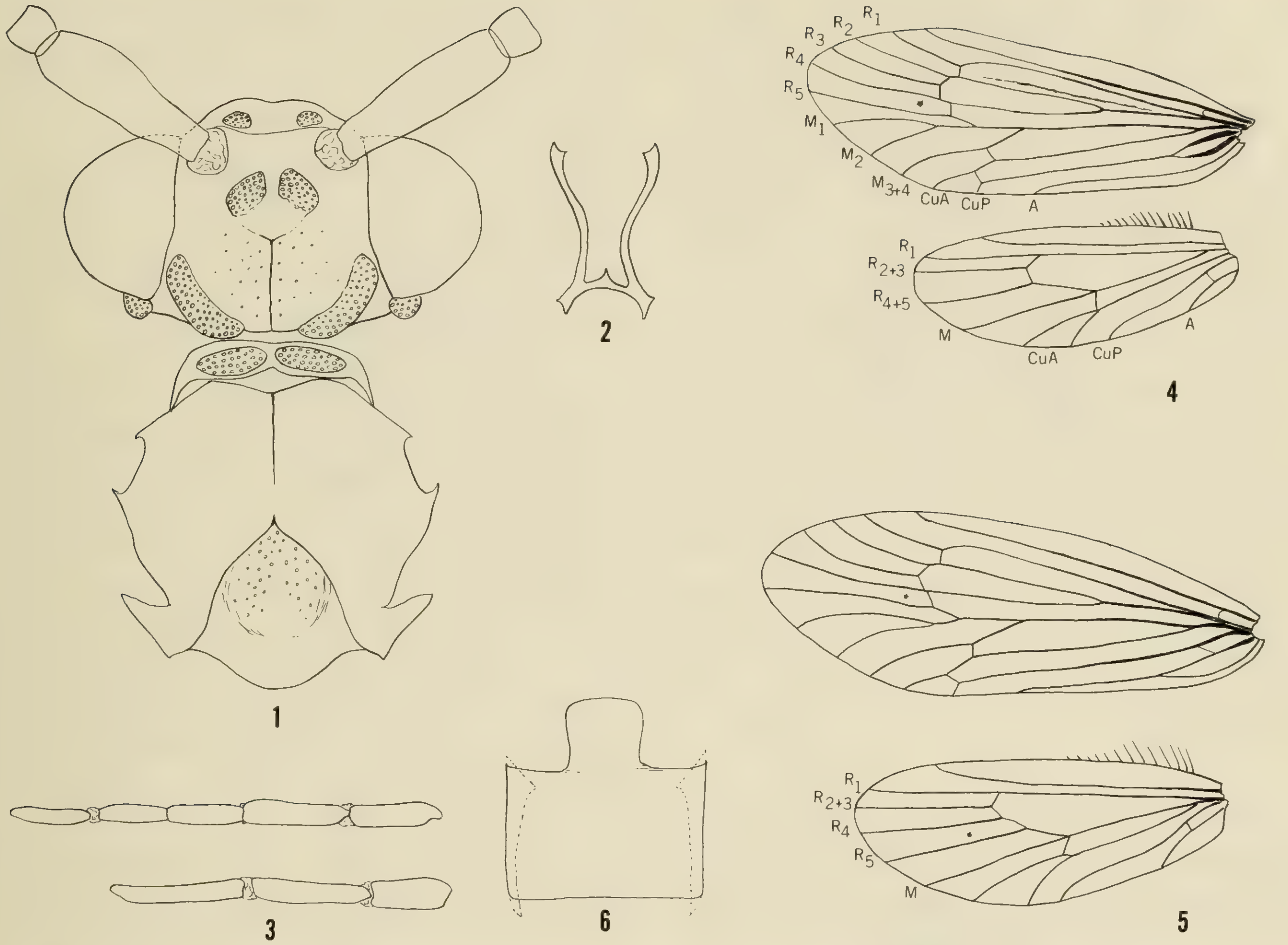
Over 35 years ago in his first large work on Neotropical caddisflies, Schmid (1955) described the first of the unusual "Sericostomatoid" genera from the Chilean Subregion. At that time he commented on the atypical structure, especially the unspecialized condition of the maxillary palpi, of some of the new taxa. In that work the genus *Eosericostoma* with two included species, *aequispina* and *inaequispina,* was described from several Chilean specimens. At about the same time, the monumental work of Mosely & Kimmins (1953) on the caddisfly fauna of Australia and New Zealand appeared. Both works recognized a large number of odd, atypical genera in the Sericostomatidae. Although Mosely & Kimmins (1953) created several families, including the Helicophidae, for certain aberrant genera, most were placed in the Sericostomatidae, which has been referred to as the "curiosity shop" of the Trichoptera (McLachlan 1876: 221). Even South Africa possesses its quota of unusual Sericostomatoids (Barnard 1934, Scott 1985). The close relationships between elements in these faunae have been recognized in Trichoptera (Ross 1967, Schmid 1990), Plecoptera (Illies 1965), Ephemeroptera (Edmunds 1972), Odonata (Watson et al. 1991) and Chironomidae (Brundin 1966).

On trips to Chile and Southwestern Argentina, I have collected adults of this genus and many larvae and pupae producing flat sand grain cases, much resembling those of the European genus *Thremma.* Many of these collections of immatures contained male and female metamorphotypes, linking the larval, pupal and adult stages of the genus *Eosericostoma.* This paper is a closer look into the structure of these three stages of *Eosericostoma* and their implication as to the correct placement of the genus.

Genus *Eosericostoma* Schmid

Eosericostoma Schmid, 1955:156.—Flint, 1974:91.

The genus contains only two species, *E. inaequispina* Schmid, the type species, and *E. aequispina* Schmid, both described when the genus was established. I have abundant



Figs. 1–6. Adult structures, *Eosericostoma inaequispina*: 1, head, antennal scape and pedicel, pronotum and mesonotum, dorsal; 2, tentorium, dorsal; 3, maxillary palpus above, and labial palpus below, lateral; 4, forewing above, and hindwing below of male; 5, forewing and hindwing of female; 6, seventh sternum of male, ventral.

material of all stages of both species. The differences between the species are apparent in both the male and female genitalia, especially after study of comparative material. However, no apparent differences were seen in the immature stages, perhaps not surprising considering the very close relationship of the two species. The following detailed generic description is based on the type species and serves equally well for *aequispina.* The specific diagnoses will contain the genitalic descriptions, the only structure by which I can discriminate between the species.

Adult

Head.—Ocelli lacking (Fig. 1). Antenna in both sexes with scape long, pedicel equidimensional, flagellum of 33–35 segments (basal segment often weakly divided). Head warts paired: small, round, posteriad to eye; long, ovoid posterolaterally; small, bean-shaped anteromesally; small, round beneath antennae. Median suture distinct on posterior half of vertex, forked anteriad, arms indistinctly encompassing anteromesal warts. Tentorium well developed, lateral arms connected posteriad by a transverse bridge, with a point mesally from anterior margin of bridge; no dorsal arms (Fig. 2). Maxillary palpi 5-segmented; labial palpi 3-segmented; identical in both sexes (Fig. 3).

Thorax.—Tibial spurs, ♂ and ♀, 2,4,4; midtibia, ♂ and ♀ with a row of short spines entire length. Wing venation dimorphic: male forewing with a vein-like thickening in cell between R_1 and Rs; CuP apparently with a small cell basally; only a single A vein (Fig. 4): female forewing with no vein-like thickening; no cell basally in Cu2; 1A and 2A looped together basally (Fig. 5). Hindwing of female with an additional vein arising from outer margin of open central cell, in front of this vein nygma present (Fig. 5); neither vein nor nygma in male. Pronotum with a pair of transverse, elongate, dorsal, setal warts. Mesoscutum without warts, with an anteromesal suture not quite reaching scutellum; mesoscutellum large, with a large, but indistinct, wart bearing setae mostly near lateral margins (Fig. 1).

Abdomen.—No basal modifications. Fifth sternum without any apparent glandular structure. Seventh sternum of male with a large, nail-like posteromesal process (Fig. 6); lacking in female.

Larva

Eruciform, abdomen strongly tapered posteriad (Fig. 7). Sclerites light brown, with pale, lightly sclerotized areas. Length to 5.5 mm. Constructing a flattened, widened, sand grain case (Fig. 9).

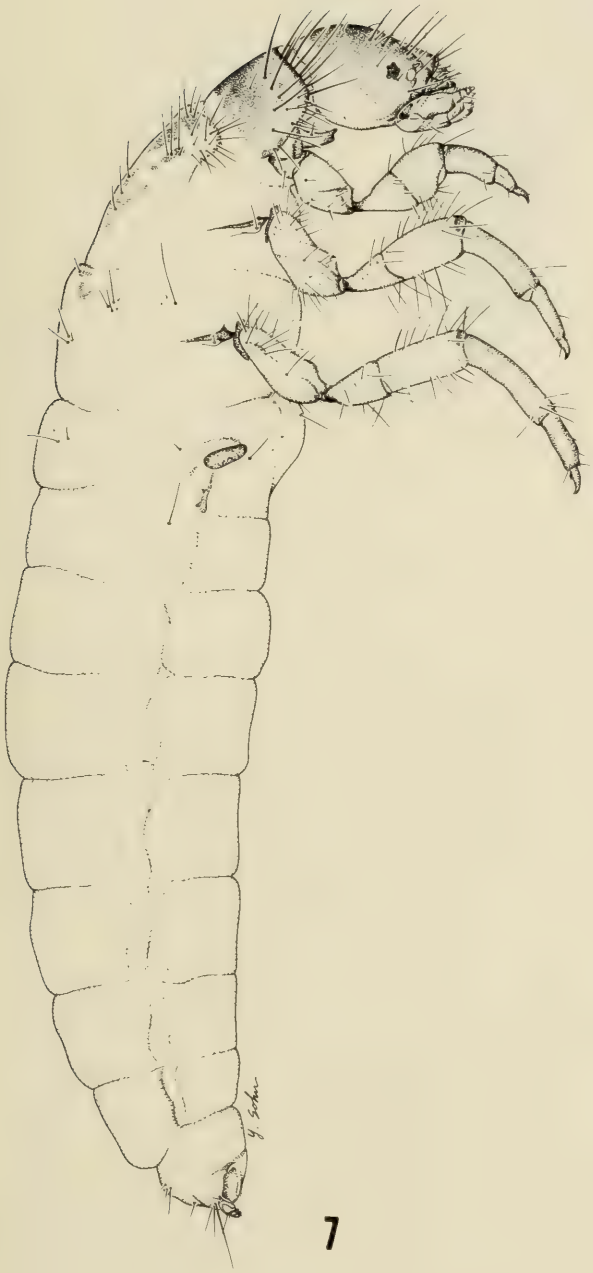
Head.—Capsule brown (Fig. 8); posteriorly and ventrally pale, unsclerotized with only muscle attachments brown; ventral apotome completely indistinguishable in pale, ventral region (in 4th and earlier instars these regions are fully sclerotized, with ventral apotome triangular in shape, heavily sclerotized anteriorly, attenuate posteriorly, not quite attaining posterior margin of genae). Head in outline, slightly elongate, without specialized features; frontoclypeal apotome slightly constricted posteriad to middle. Most primary setae clearly present; 13 and 17 minute or absent; 8 and 18 not found. Antenna nearer anterior margin of gena than eye.

Labrum a bit wider than long, lateral margin rounding into anterior margin, with a marginal fringe of short hair; setae 5 and 6 erect, dark, 2,3,4 shorter and pale (Fig. 10). Mandibles symmetrical, trianguloid; apex entire, with a deep apicomesal groove; mesal brush well developed; pair of basal, external setae inserted dorsolaterally (Fig. 11). Maxillolabium elongate, submental sclerite curved mesally and then apicad along lateral margin of mesal region; galeal lobe large, membranous, densely covered with short hair; oral surface of labium produced into a large, hairy, membranous lobe (Fig. 12).

Thorax (Fig. 8).—Pronotum brown; posterior margin unsclerotized and pale (sclerotized in early instars); anterior margin of each half bearing about 9 large setae; a second row of 3 setae running laterad at about ⅓ of distance from front to rear of sclerite; another 10–12 smaller lateral setae. Trochanter elongate, nearly truncate apically with apicodorsal angle slightly produced; bearing a large, basodorsal seta (Fig. 13). Mesonotum with many dark, sclerotized areas bearing a few scattered setae, especially anterolaterally; division between meso- and metanota very indistinct. Metanotum with Sa1 bearing a small sclerotization and a small seta or two; Sa2 with a large and several small setae; Sa3 with about 6 setae. No sternal processes or setae.

All legs in general with coxae, trochanters and femora rather hairy; tibiae and tarsi with a few apical setae (Fig. 13). Foreleg with femur short and broad; ventral margin of trochanter and femur with well developed fringe; a pair of apicoventral spines on tibia. Midleg with sparse, short, pale trochanteral fringe; single apicoventral spine on tibia. Hindleg with sparse, short, pale trochanteral fringe; apicoventral seta of tibia, hairlike.

Abdomen (Fig. 7).—First segment with lateral humps well developed, dorsal hump lacking. Lateral hump capped by a large, dense patch of dark spicules, and a linear sclerite extending posteriad into the fold between segments 1 and 2. First segment with few setae dorsally, 1 immediately above and another beneath lateral hump, and submesal pair ventrally. Second segment with 1 large, anterolateral seta extended over lat-



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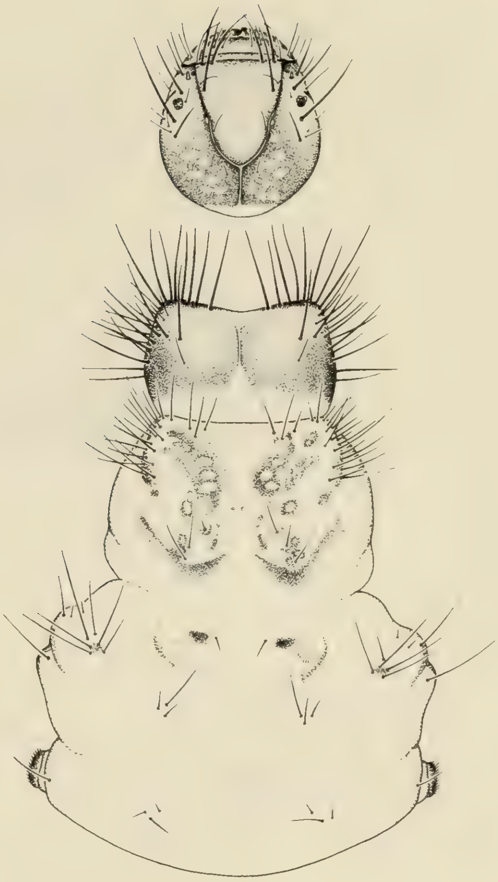

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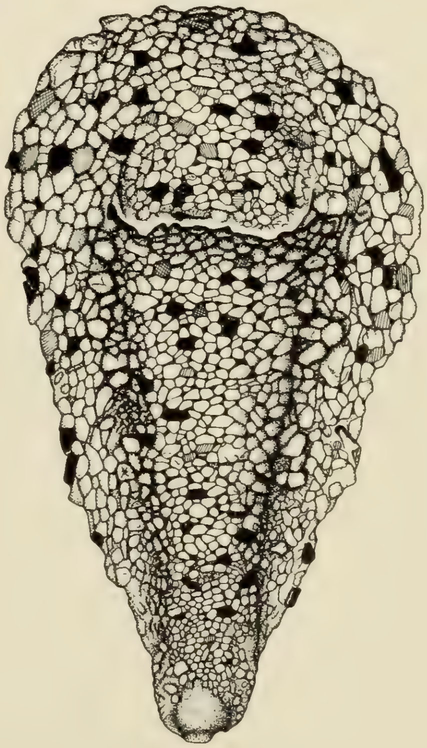

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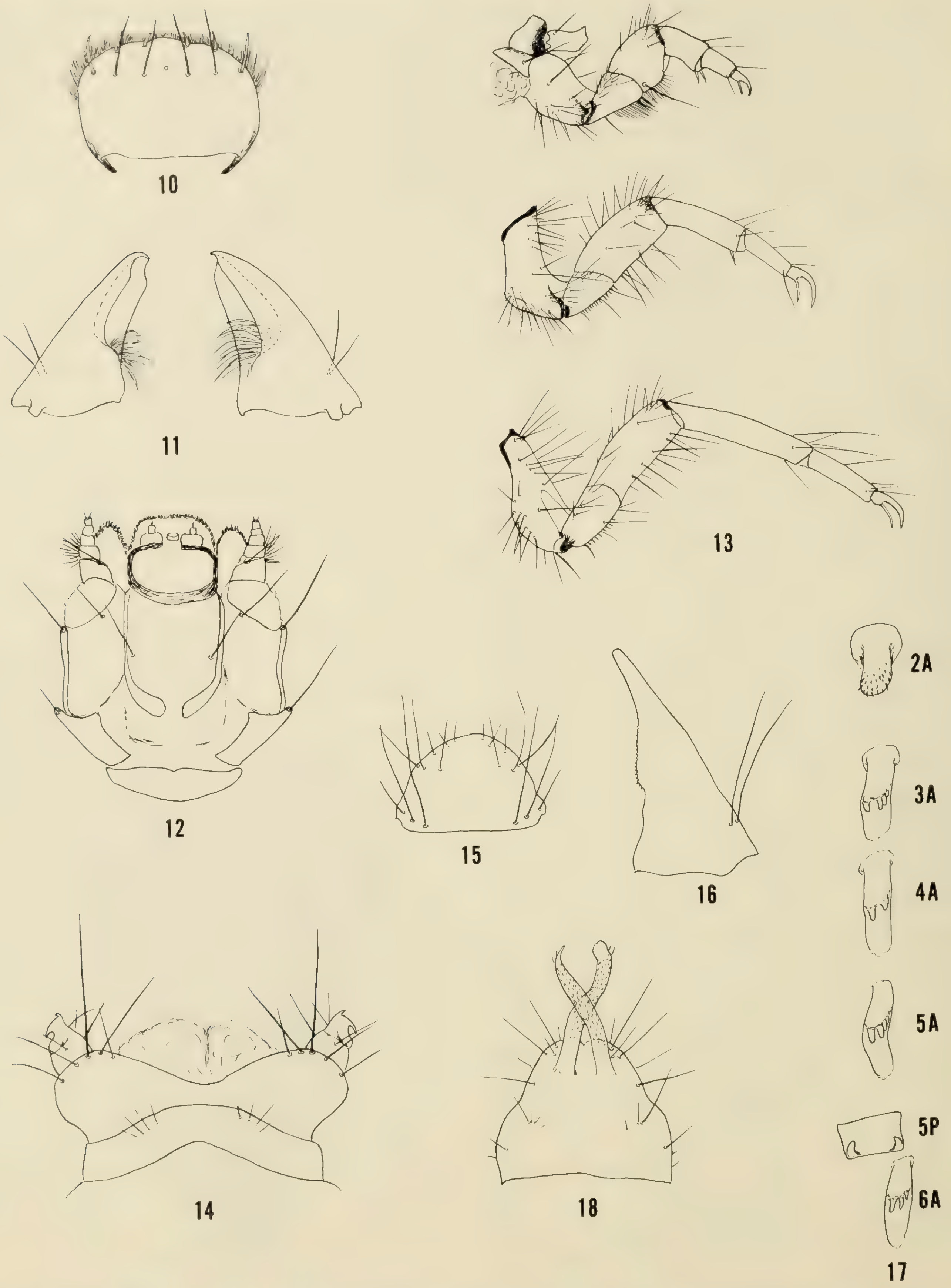
Figs. 7–9. *Eosericostoma inaequispina*: 7, larva, lateral; 8, larval head and thorax, dorsal; 9, larval case, ventral.



Figs. 10–18. *Eosericostoma inaequispina*: 10, larval labrum, dorsal; 11, larval mandibles, dorsal; 12, larval maxillolabium, ventral; 13, larval foreleg, midleg, hindleg, respectively top to bottom, lateral; 14, apex of abdomen, dorsal; 15, pupal labrum, dorsal; 16, pupal mandible, dorsal; 17, pupal hook plates, dorsal (2–6 = abdominal segment number, A = anterior, P = posterior); 18, apex of pupal abdomen, dorsal (tip of process curving to left shown in profile).

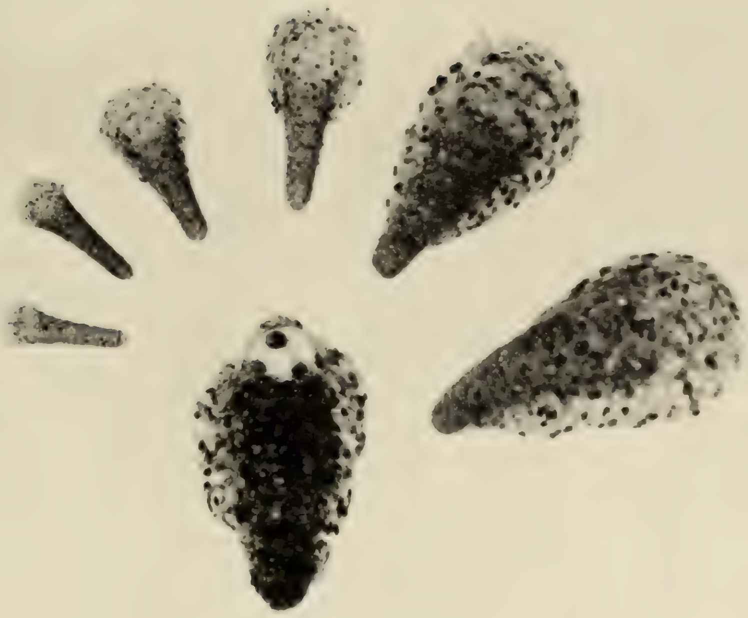


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Fig. 19. *Eosericostoma inaequispina,* larval cases in top row showing change in form with increasing size; pupal case below showing anterodorsal opening left by exit of pupa.

eral hump. No gills or lateral line. Eighth segment with lateral row of several dozen, very small, bifid processes. Ninth tergum without sclerotized plate, but with few setae posteriorly. Anal prolegs mostly fused to apex of abdomen, with few setae, 1 of which is very long and dark. Anal claw small, with single, very small, dorsal tooth (Fig. 14).

Larval case.—Up to 7 mm long, by 4 mm wide. Constructed of small sand grains; in some collections sand grain sized fragments of leaf are used wholly or in part alternating with sand. Consisting of a central tube on ventral face with a broad, hoodlike, anterior extension from dorsal surface that is continuous along sides, but becomes narrower posteriad (Fig. 9). Posterior apex of case silken ventrally, ending in a round, slightly upturned, central opening strongly rimmed with silk. Smallest cases mostly a simple tube with the anterior, hoodlike extension barely extended along sides, with passing instars lateral flanges enlarged, and case becomes rounded in outline (Fig. 19); posterior silken closure and central opening unchanged.

Pupa

The pupa is exarate; white until the developing adult turns color inside the cuticle. Length of body 4.5–5.5 mm.

Head.—Labrum semicircular; with 3 paired, basolateral bristles, 3 more at midlength on each side and 2–3 small setae along anterolateral margin (Fig. 15). Mandibles about twice as long as wide basally; inner margin minutely serrate for central third of its length; with 2 large basolateral bristles (Fig. 16). Face with 1 bristle beneath eye, 1 at anteroventral margin of eye, 2 pairs ventrally on face, 1 pair between antennal bases, 2 pairs on vertex (1 more anteromesad, other more posterolaterad). Antenna extended posteriad alongside body, apices extended slightly beyond tip of abdomen; scape with 2 bristles dorsally.

Thorax.—Meso- and metanota each with 2 pairs of dorsal bristles (metanotum sometimes apparently lacking anterior pair). Wing sheaths not reaching apex of abdomen. Coxae of fore- and midlegs each with a large bristle; tarsi of fore- and midlegs with lateral swimming fringes; apices of hindlegs surpassing tip of abdomen (coequal to tips of antennae).

Abdomen.—Lacking gills. Lateral fringe commencing posteriorly on segment 6, curving ventrad on segments 7 and 8. Hook plates present anteriorly on segments 2 through 6, posteriorly on 5; plate 2A rounded, knoblike with many small spicules; plates 3A–6A each elongate, narrow, 2–4 hooks borne at midlength on a low ridge; 5P rectangular, with a hook borne from both posterolateral angles (Fig. 17). Segments 7–9 each with 1–3 bristles dorsolaterally, each genital lobe with 5–6 bristles. Apical processes long, slender, crossing over each other at midlength, covered with many, small spicules; tip flattened, without long bristles (Fig. 18).

Pupal case.—Essentially like that of larva, slightly modified. A silken, parchment-like, anterior extension of ventral tubular portion reaching anterior margin of dorsal shield, most of pupal head and thorax found in this area (this tube also attaches case to substrate on its ventral surface); at anterior end of this extension a narrow, transverse slit is left open next to dorsal hood, slit margined with a slight (to heavy) rim of silk. Posterior end of case modified by extension of sand grain flange completely around end, leaving an anteapical round (to oval), rimmed, silken opening dorsally. Pupa usually found with venter toward substrate; several pupae preserved in process of cutting escape opening, now with venter dorsad cutting opening anteriorly in dorsal wall of sand grain case (many empty cases found with circular opening in this position, suggesting this is normal way of eclosion, Fig. 19).

Key to Species, Adults

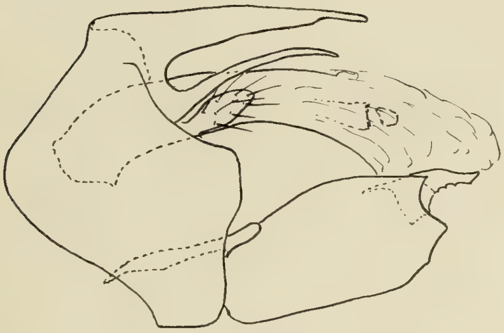
1. Apex of abdomen with claspers, tenth tergites, phallus extending freely: males 2
– Apex of abdomen almost semicircular in outline, no free processes: females 3
2. Clasper in ventral aspect with inner margin curving irregularly toward lateral margin at its apex; dorsal surface with its apical process near inner margin, slender (several times as long as wide) .... *inaequispina*
– Clasper in ventral aspect with inner margin sharply angled near apex, then extending nearly straight to lateral margin; dorsal surface with apical process near center, broader (barely longer than broad) .. *aequispina*
3. Vaginal sclerite with its apicolateral, bandlike supports attached near posterior margin and running more or less directly to a bilobate structure almost attaining apex of terminal segment .... *inaequispina*
– Vaginal sclerite with its supports attached midlaterally, then curving distinctly mesad, ending before a knobbed, internal plate attached to a bilobate structure only extending half length of terminal segment .. .. *aequispina*

Eosericostoma inaequispina Schmid
Figs. 1–22, 26, 28

Eosericostoma inaequispina Schmid, 1955: 156.—Flint, 1974:91.

Eosericostoma aequispina Schmid.—Schmid, 1957:394 [misidentification, in part—series from Tregalemu]; 1964:339 [misidentification, in part—series from Curacautín, and series from Pillim-Pilli mixed].

A rather common and widespread species, especially in Chile. The species are only to be told apart with certainty by a careful study of the genitalia, either male or female, as outlined in the key. Pinned material of this species appears to be browner and larger, on average, than does the following spe-



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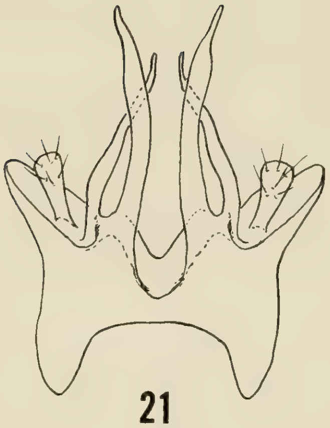

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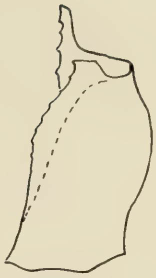

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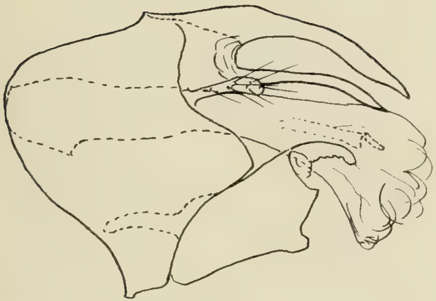

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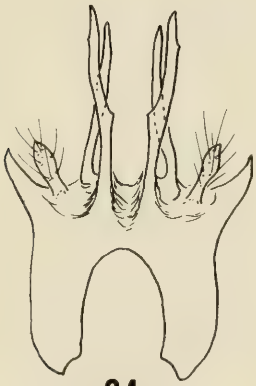

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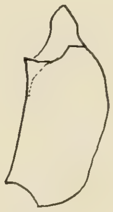

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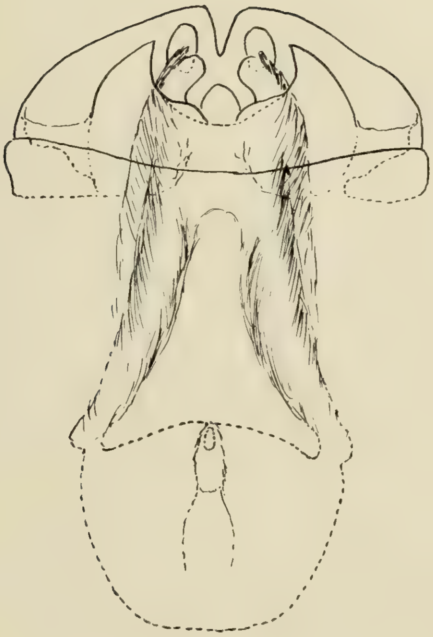

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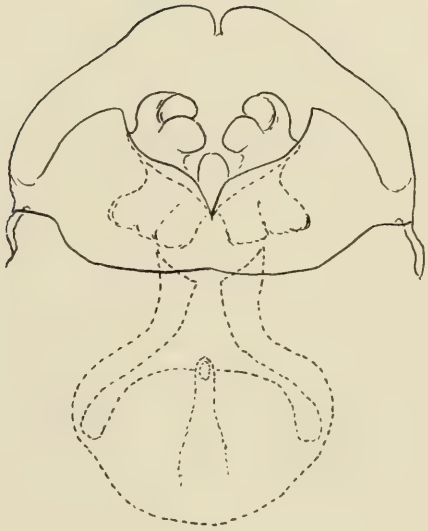

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Figs. 20–27. *Eosericostoma inaequispina*: 20, male genitalia, lateral; 21, male ninth and tenth terga and cerci, dorsal; 22, male clasper, ventral. *Eosericostoma aequispina*: 23, male genitalia, lateral; 24, male ninth and tenth terga and cerci, dorsal; 25, male clasper, ventral. *Eosericostoma inaequispina*: 26, female genitalia, lateral. *Eosericostoma aequispina*: 27, female genitalia, lateral.

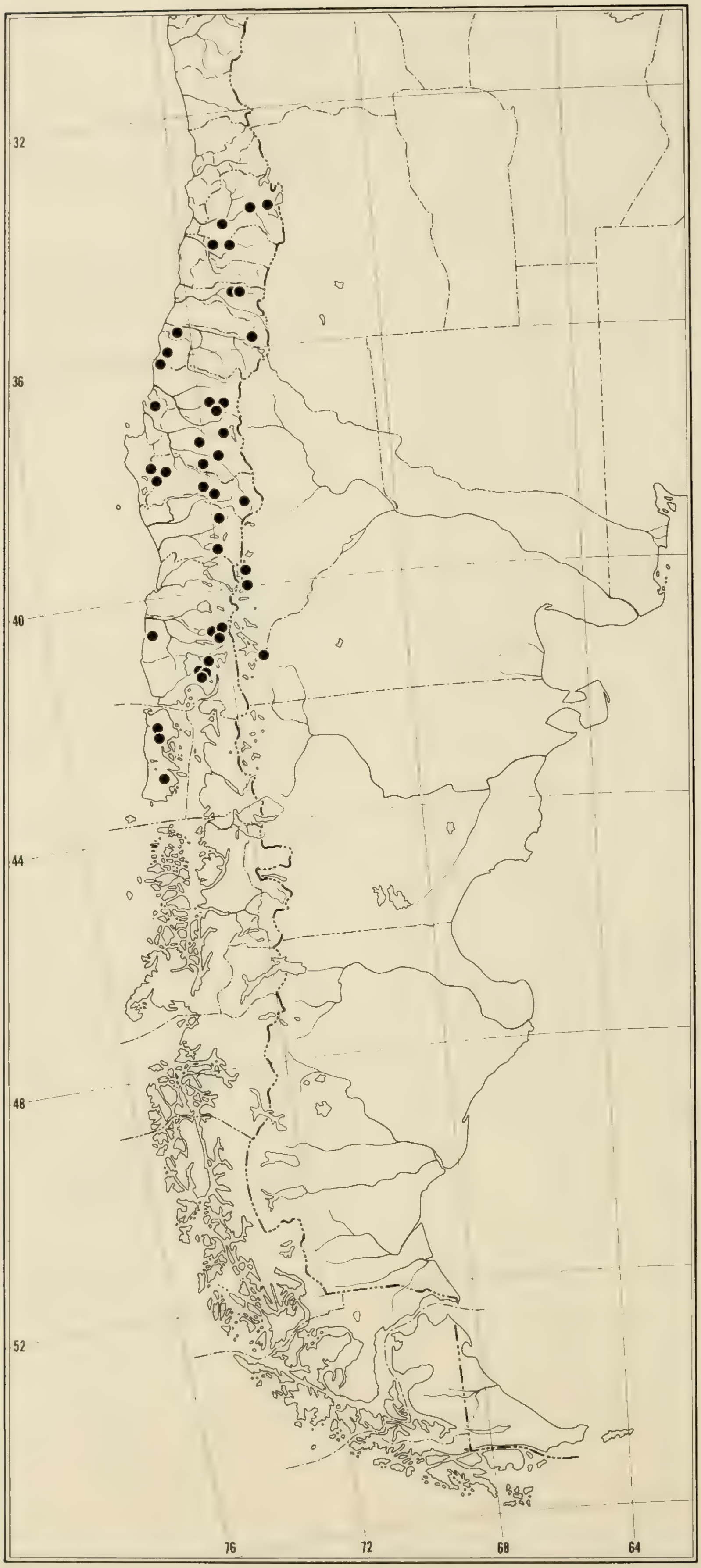

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Fig. 28. *Eosericostoma inaequispina*, known distribution in Chile and Argentina.

cies, although this will not serve to distinguish any two individuals.

Adult.—Length of forewing, 5–8 mm. Color uniformly brownish-gray. Male genitalia. Ninth segment annular, both anterior and posterior margins convex laterally. Tenth tergum divided mesally into lateral halves, each of which is divided in long, slender dorsal and ventral processes extended posteriad and pointed apically. Cercus elongate, clavate. Clasper in lateral aspect about twice as long as high, apically with a small lateral angle and a mesodorsal process; in ventral aspect with ventromesal margin apically curving to lateral margin, with a small apical lobe, dorsal process much longer than wide and arising from mesal margin. Phallus elongate, tubular, sclerotized basally, membranous apically with a small, internal, phallotremal sclerite. Female genitalia. Ninth sternum connected laterally to venter of combined ninth and tenth terga, and apicolaterally almost attaining tip of abdomen, with apicomesal margin sinuate, indistinct mesally. A small, lightly sclerotized, mesal lobe extending posteriad of ninth sternum, and flanked laterally by a bilobate structure. Apex of tenth tergum divided mesally. Internally with a darkened band-like sclerite extending anteriad from lateral margin of bilobate structure and attached to vaginal sclerite near its posterolateral angle. Vaginal sclerite large, shield-shaped, with a small posteromesal opening in a caliper-like central structure.

Material examined.—Holotype, male: Chili (Santiago) El Manzano 9-II-1950 L. E. Peña [now Chile, Prov. Cordillera, El Manzano, 9 Feb 1950, L. E. Peña G.] NMNH Type 71842.

Argentina, Prov. Neuquén: Brooklet at Lago Huechulafquén, 26 Jan 1974, O. S. Flint, Jr., 1 ♂; 5 km NW Lago Lolog, 22 Jan 1974, O. S. Flint, Jr., 2 ♂. Prov. Río Negro: Bariloche, 4 Feb 1962, T. Cekalovic, 1 ♂, 1 ♀.

Chile, Prov. Arauco: Pillim-Pilli, 2–5 Feb 1959, L. E. Peña G., 3 ♂, 2 ♀ [Schmid determined *aequispina*]. Prov. Bío-Bío: Caledonia, E Mulchén, 700–900 m, 6–15 Feb 1981, L. E. Peña G., 3 ♂, 6 ♀; Estero Huequecura, 25 km E Santa Bárbara, 24 Jan 1978, C. M. & O. S. Flint, Jr., 2 ♂; El Abanico, 1100 m, 17–19 Mar 1984, L. E. Peña G., 5 ♂, 12 ♀; Río Duqueco, Hacienda San Lorenzo, E Los Angeles, 100 m, 20–23 Jan 1991, L. E. Peña G., 1 ♂, 12 ♀. Prov. Cachapoal: Bajo Los Maitenes, NW Rancagua, 1600 m, Jan–Feb 1982, L. E. Peña G., 4 ♂, 2 ♀; Cerro La Matancilla, Cordillera Costa, 1750 m, 8–10 Jan 1982, L. E. Peña G., 1 ♂, 2 ♀. Prov. Cauquenes: Alto Tregualemu, ca. 20 km SE Chovellén, 500 m, 26–27 Jan 1979, D. R. Davis et al., 1 ♀; same, but 1–4 Dec 1981, L. E. Peña G., 1 ♂; same, but 10 Dec 1953, L. E. Peña G., 1 ♂ [Schmid determined *aequispina*]; Paso Garcia, ca. 23 km NW Cauquenes, 300 m, 29–30 Nov 1981, D. R. Davis, 3 ♂, 2 ♀. Prov. Cautín: Truful Truful, E Volcán Llaima, Conguillo National Park, 700 m, 12–13 Jan 1989, L. E. Peña G., 3 ♀; near Pucón, 4 Jan 1966, Flint & Cekalovic, 14 pupae & prepupae (including 3 ♂ metamorphotypes), 7 empty pupal cases. Prov. Chiloé: Huequetrumao, 25 km N Quellén, 50 m, 26–27 Dec 1981, D. R. Davis, 2 ♂, 1 ♀; Puntra, ca. 30 air km S Ancud, 50 m, 20–23 Dec 1981, D. R. Davis, 2 ♀; same, but 15 Dec 1985, L. E. Peña G., 1 ♂, 1 ♀; Piruquina, 15 Mar 1987, L. E. Peña G., 1 ♀; Río Cude, Pudguapi, ca. 15 km NW Castro, 20 Jan 1987, C. M. & O. S. Flint, Jr., 3 ♀. Prov. Concepción: Quebrada Honda near Lirquén, 31 Dec 1966, Flint & Cekalovic, 2 ♂; same, but 5 Feb 1966, T. Cekalovic K., 1 ♂. Prov. Cordillera, El Alfalfal, 1320 m, 29 Feb 1968, Flint & Peña, 1 ♂, 4 ♀; same, but 12–13 Oct 1969, Flint & Barria, 60 larvae, 1 prepupa, 2 empty pupal cases; same, but 22 Jan 1978, C. M. & O. S. Flint, Jr. & P. J. Spangler, 6 pupae & prepupae (including ♂ & ♀ metamorphotypes), 4 empty pupal cases. Prov. Curico: Las Tablas, E Curico, Feb 1985, L. E. Peña G., 9 ♂, 7 ♀; Río Teno, ca. 40 km E Curico, 25–27 Nov 1981, D. R. Davis, 2 ♂, 1 ♀. Prov. Llanquihue: Salto Chamiza, Correntoso, 100 m, 19 Jan 1987, C. M. &

O. S. Flint, Jr., 1 ♂, 1 ♀; Lago Chapo, Correntoso, 16–17 Feb 1990, L. E. Peña G., 1 ♂, 3 ♀; El Chingue, N Correntoso (S Volcán Calbuco), 300 m, 20–25 Jan 1980, L. E. Peña G., 2 ♂, 1 ♀; Petrohué, Lago Todos Los Santos, 600 m, 1–3 Jan 1982, Davis & Peña, 1 ♂, 4 ♀; Hornohuinco, 11 km SW Lago Chapo, 300 m, 29–31 Dec 1981, Davis & Peña, 2 ♂, 11 ♀. Prov. Malleco: Vegas Blancas, 27 km W Angol, 700 m, 17 Jan 1987, C. M. & O. S. Flint, Jr., 2 ♂, 1 ♀; Curacautín, 27–28 Jan 1959, L. E. Peña G., 1 ♂, 4 ♀ [Schmid determined *aequispina*]; Río Manzanares [ca. 10 km W Purén], 2 Jan 1966, Flint & Cekalovic, 1 ♂, 8 larvae, 48 pupae and prepupae (including ♂ & ♀ metamorphotypes), 32 empty pupal cases; E Lonquimay, 1000 m, 21–23 Dec 1976, L. E. Peña G., 3 ♂, 1 ♀; near Victoria, 25 Nov 1957, J. Illies #110E, 1 ♀ metamorphotype. Prov. Mellipilla: La Viluma, SE Mellipilla, 350 m, 15–17 Dec 1987, L. E. Peña G., 2 ♂, 3 ♀. Prov. Ñuble: Las Trancas, 21 km E Recinto, 1300 m, 17 Jan 1979, D. R. Davis et al., 2 ♀; same, but 2 Mar 1968, Flint & Peña, 1 ♂; Río Chillán, near Recinto, 6 Mar 1968, Flint & Peña, 4 ♂, 5 ♀; Atacalco, Recinto, 700 m, 17–18 Dec 1976, L. E. Peña G., 1 ♀. Prov. Osorno: Río Chanleufú, 1 km S Aguas Calientes, 8–9 Feb 1978, C. M. & O. S. Flint, Jr., 1 ♂, 1 ♀; Lago El Toro, Parque Nacional Puyehue, 7–8 Feb 1978, C. M. & O. S. Flint, Jr., 6 ♂, 10 ♀; same, but Aguas Calientes, 400 m, 4–5 Jan 1982, L. E. Peña G., 1 ♂, 2 ♀; same, but 5–7 Mar 1984, 1 ♀; same, but Anticura, 5–18 Jan 1986, L. E. Peña G., 1 ♀; Tril-Tril, S Pucatrihue, 1–10 Feb 1980, L. E. Peña G., 1 ♀. Prov. Talca: El Patanillo, 17 km SE Constitución, 350 m, 28 Nov 1981, D. R. Davis, 2 ♀; Los Cipresses, 13–15 Jan 1968, L. E. Peña G., 3 ♂.

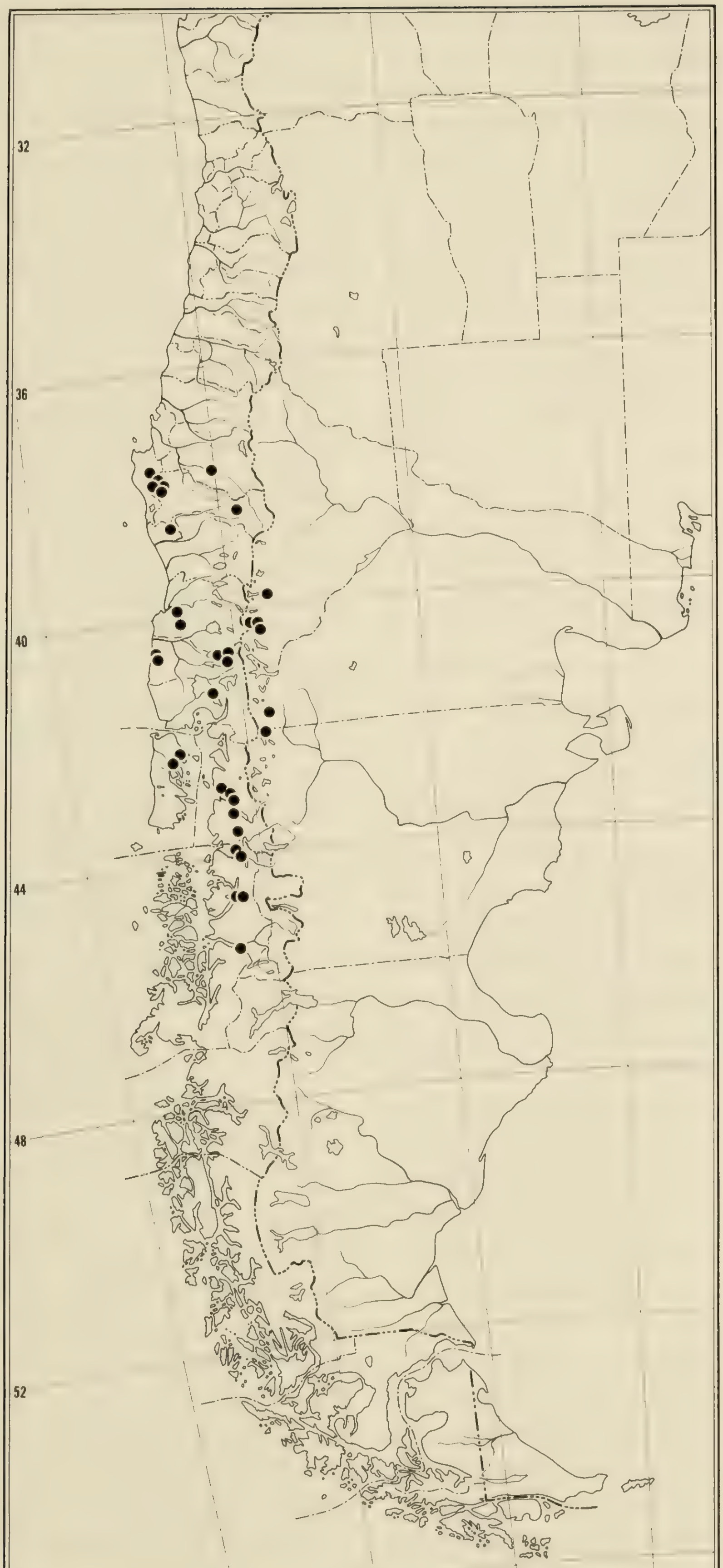
Eosericostoma aequispina Schmid
Figs. 23–25, 27, 29

Eosericostoma aequispina Schmid, 1955: 156; 1957:394; 1958:209; 1964:339.—Flint, 1974:91.

The only certain manner to distinguish this species from the preceeding is by the genitalia, as discussed in the key and shown in the illustrations. A long pinned series of this species appears to the naked eye to be darker gray, with the specimens a bit smaller on the average than in *inaequispina,* although there is a total overlap in both categories.

Adult.—Length of forewing, 5–7 mm. Color uniformly gray. Male genitalia. Ninth segment annular, both anterior and posterior margins convex laterally, that of posterior margin large and angular. Tenth tergum divided mesally into lateral halves, each of which is divided in long, slender dorsal and ventral processes extending posteriad and pointed apically. Cercus elongate, clavate. Clasper in lateral aspect about twice as long as high, apically with small lateral and ventral angles and a mesodorsal process; in ventral aspect with ventromesal margin ending apically in a sharp apicomesal angle, from which margin runs almost straight laterad, dorsal process barely longer than wide and arising from center of apical margin. Phallus elongate, tubular, sclerotized basally, membranous apically with a small, internal, phallotremal sclerite. Female genitalia. Ninth sternum connected laterally to venter of combined ninth and tenth terga, and apicolaterally extending only half length of ninth and tenth terga, with apical margin sinuate, indistinct mesally. A small, lightly sclerotized, mesal lobe extending posteriad of ninth sternum, and flanked laterally by a bilobate structure. Apex of tenth tergum slightly divided mesally. Internally with a quadrate, slightly convoluted plate attached internally to bilobate structure, a band-like sclerite extending anteriad from internal plate, curved sharply laterad anteriorly and attached to vaginal sclerite laterally near its midlength. Vaginal sclerite large, shield-shaped with a small posteromesal opening in a caliper-like central structure.

Material examined.—Holotype, male: Chili (Chiloé) Aucar, 6-I-1952, L. E. Peña



29

Fig. 29. *Eosericostoma aequispina,* known distribution in Chile and Argentina.

[now Chile, Prov. Chiloé, Aucar, 6 Jan 1952, L. E. Peña G.]. NMNH Type 71840.

Argentina, Prov. Chubut: Arroyo Golondrinas, 6 km N Lago Puelo, 8 Feb 1974, O. S. Flint, Jr., 36 ♂, 11 ♀, 15 larvae, 79 pupae and prepupae (including ♂ & ♀ metamorphotypes), 7 empty pupal cases. Prov. Neuquén: 13 km E Quila Quina, 27 Jan 1974, O. S. Flint, Jr., 10 ♂, 1 ♀; brooklets at Lago Meliquina, 25 Jan 1974, O. S. Flint, Jr., 26 ♂, 24 ♀; 5 km E Lago Huechulafquén, 26 Jan 1974, O. S. Flint, Jr., 1 ♂, 1 larva, 28 pupae and prepupae (including 1 ♀ metamorphotype), 4 empty pupal cases; canal, Estación Forestal Pucará, 28–29 Jan 1974, O. S. Flint, Jr., 4 ♂; same, but 3–5 km W, 30 Jan 1974, 3 ♂; same, but Río Nonthué, 28–31 Jan 1974, 2 ♂; same, but Pantano, 29 Jan 1974, 16 ♂, 10 ♀. Prov. Río Negro: 5 km S Río Villegas, 7 Feb 1974, O. S. Flint, Jr., 1 ♀.

Chile, Prov. Aisén: Puerto Cisnes, Feb 1961, L. E. Peña G., 1 ♂; Río Cisnes, 10 km E Puerto Cisnes, 25 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♂; Río Riesco, S Puerto Aisén, 10 Feb 1990, L. E. Peña G., 1 ♂, 1 ♀; 10 km S La Junta, 26 Jan 1987, C. M. & O. S. Flint, Jr., 3 ♂, 1 ♀; 20 km S La Junta, 26 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♀. Prov. Arauco, Pillim-Pilli, 2–5 Feb 1959, L. E. Peña G., 1 ♂; Pichinahuel, 1–30 Jan 1959, L. E. Peña G., 2 ♂; W Pichinahuel, Cordillera Nahuelbuta, 900 m, 14–16 Jan 1988, L. E. Peña G., 1 ♂; Chacay, 11 Feb 1953, L. E. Peña G., 1 ♂; Carámavida, 25–31 Dec 1953, L. E. Peña G., 1 ♂; same, but 3–31 Jan 1967, 1 ♂, 1 ♀. Prov. Bío-Bío: Santa Bárbara, 6 Feb 1958, L. E. Peña G., 1 ♂. Prov. Cautín: Chacamo, NE Nueva Imperial, 600–700 m, 11–23 Feb 1981, L. E. Peña G., 1 ♀. Prov. Chiloé: Aucar, 6 Jan 1952, L. E. Peña G., 2 ♂ paratypes; Dalcahue, 10–20 Feb 1957, L. E. Peña G., 7 ♂, 4 ♀. Prov. Llanquihue: El Chingue, N Correntoso (S Volcán Calbuco), 300 m, 20–25 Jan 1980, L. E. Peña G., 3 ♂, 6 ♀. Prov. Malleco: Cordillera Nahuelbuta, Cabreria, 1100 m, 15–20 Jan 1977, L. E. Peña G., 1 ♂; Cordillera Nahuelbuta, Los Gringos Camp, 1300 m, 29 Jan–5 Feb 1979, Davis et al., 3 ♂, 5 ♀; same, but 1100 m, 5–9 Jan 1989, L. E. Peña G., 2 ♂, 3 ♀; Cordillera de las Raices, 40 km E Curacautín, 1200 m, 6–7 Feb 1979, Davis et al., 1 ♂. Prov. Osorno: Pucatrihue, 26–31 Jan 1980, L. E. Peña G., 1 ♂, 1 ♀; same, but 26–30 Jan 1978, C. M. & O. S. Flint, Jr., 2 ♂; Pulamemo, E Bahia Blanca, 30 Jan 1978, C. M. & O. S. Flint, Jr., 2 ♂; Puyehue, 10 Feb 1979, L. E. Peña G., 1 ♂; Parque Nacional Puyehue, Río Pescadero, 7 Feb 1978, C. M. & O. S. Flint, Jr., 1 ♀; same, but Lago El Toro, 7–8 Feb 1978, 2 ♂; same, but Anticura, 28–31 Dec 1985, L. E. Peña G., 1 ♂; same, but 5–10 Jan 1986, 1 ♀; same, but Río Anticura, 31 Jan–13 Feb 1978, C. M. & O. S. Flint, Jr., 56 ♂, 66 ♀; same, but 3 km E Río Anticura, 3 Feb 1978, 9 ♂, 20 ♀; same, but Salto del Indio, 1–2 Feb 1978, 2 ♂, 4 ♀, 2 dead larvae, 18 pupae (including ♂ & ♀ metamorphotypes), 6 empty pupal cases; same, but Río Golgol, 2 Feb 1978, 2 ♂, 1 ♀; same, but brooklets, 2 km S Aguas Calientes, 9 Feb 1978, 31 pupae and prepupae (including ♂ & ♀ metamorphotypes), 10 empty pupal cases; same, but Aguas Calientes, 6 Feb 1978, 5 ♂, 3 ♀, 11 pupae and prepupae (including ♂ & ♀ metamorphotypes), 3 empty pupal cases; same, but 1 km S Aguas Calientes, Río Chanleufú, 8–9 Feb 1978, 32 ♂, 16 ♀; same, but 12 Feb 1979, Davis et al., 1 ♀; same, but Aguas Calientes to 2 km S, 600 m, 10–22 Feb 1979, 2 ♂, 8 ♀. Prov. Palena: Camping Arrayanes, 5 km NW Chaitén, 21 Jan 1987, C. M. & O. S. Flint, Jr., 6 ♂, 4 ♀; Termas Amarillo, ca. 30 km SE Chaitén, 250 m, 22 Jan 1987, C. M. & O. S. Flint, Jr., 6 ♂, 4 ♀; Río Amarillo, ca. 28 km SE Chaitén, 23 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♀; Río Caballo Muerto, 4 km N Puerto Cardenas, 23 Jan 1987, C. M. & O. S. Flint, Jr., 2 ♂; Río Ventisquero, 16 km S Puerto Cardenas, 23–24 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♀; 22 km S Santa Lucia, 24 Jan 1987, C. M. & O. S. Flint, Jr., 1 ♀. Prov. Valdivia: Las Trancas, W La Unión, 500 m, 5–10 Feb 1988, L. E. Peña G., 2 ♀; Rincón de la Piedra, ca. 20 km SE

Valdivia, 30 m, 24–25 Feb 1979, Davis et al., 4 ♀.

Eosericostoma species

Here are listed those larvae and pupae that are not unequivocally identifiable to species.

Material examined.—Argentina, Prov. Neuquén: 13 km E Quila Quina, 27 Jan 1974, O. S. Flint, Jr., 1 prepupa; Arroyo Pilpil, near San Martín de los Andes, 22 Feb 1978, C. M. & O. S. Flint, Jr., 3 empty pupal cases. Prov. Río Negro: 5 km S Río Villegas, 7 Feb 1974, O. S. Flint, Jr., 2 empty pupal cases.

Chile, Prov. Arauco: Carámavida, 17–19 Oct 1969, Flint & Barria, 3 larvae; San Alfonso above Carámavida, 16–17 Oct 1969, Flint & Barria, 28 larvae, 1 empty pupal case. Prov. Chiloé: Río Butalcura, 21 Oct 1969, Flint & Barria, 1 larva. Prov. Concepción: Quebrada Honda, near Lirquén, 14–15 Oct 1969, Flint & Barria, 1 larva. Prov. Llanquihue: Río Gomez, 6 Jan 1966, Flint & Cekalovic, 1 larva, 1 empty pupal case. Prov. Malleco: Parque Nacional Contulmo, 2 Jan 1966, Flint & Cekalovic, 2 larvae; Vegas Blancas, 27 km W Angol, 700 m, 17 Jan 1987, C. M. & O. S. Flint, Jr., 1 pupa, 1 empty pupal case. Prov. Osorno: Pucatrihue, 26–30 Jan 1978, C. M. & O. S. Flint, Jr., 2 empty pupal cases; Pulamemo, E Bahia Mansa, 30 Jan 1978, C. M. & O. S. Flint, Jr., 8 pupae and prepupae, 9 empty pupal cases; Parque Nacional Puyehue, Estero el Gringo, 13 Feb 1978, C. M. & O. S. Flint, Jr., 1 pupa. Prov. Palena: Río Caballo Muerto, 4 km N Puerto Cardenas, 24 Jan 1987, C. M. & O. S. Flint, Jr., 2 pupae, 3 empty pupal cases; Río Amarillo, ca. 28 km SE Chaitén, 23 Jan 1987, C. M. & O. S. Flint, Jr., 2 pupae, 8 empty pupal cases. Prov. Talca: Alto Vilches, 29–31 Oct 1969, O. S. Flint, Jr., 30 larvae, 1 empty pupal case. Prov. Valdivia: Río Llollehue, 5 Jan 1966, Flint & Cekalovic, 18 larvae, 4 prepupae, 6 empty pupal cases; Punucapa, Fundo Walper, 3 Nov 1957, J. Illies, 3 larvae, 2 pupae; riachuelo, Fundo Walper, 16 Feb 1958, J. Illies, 4 empty pupal cases; Río Llancahue, 11 Feb 1958, J. Illies #173T, 2 empty pupal cases.

Discussion

Starting in 1967, Ross segregated many of the "Sericostomatoid" genera from Australia and New Zealand into new families. This process was given further impetus by the work of Neboiss, especially that on the Tasmanian caddisflies (Neboiss 1977) and his recent atlas (Neboiss 1986), which has resulted in the transfer of all "Sericostomatoid" genera to various notogean families and thus the removal of the Sericostomatidae from the Australasian Region. A similar process is happening in South Africa (Scott 1985), although a great deal of this work has not yet been published. In recent years a number of Chilean genera have been recognized as belonging to various Australasian "Sericostomatoid" families: *Trichovespula* and *Charadropsyche* to the Tasimiidae (Flint 1969), *Rhyncopsyche* to the Kokiriidae (Ross 1967, Neboiss 1974), *Alloecentrellodes, Austrocentrus, Eosericostoma, Microthremma* and *Pseudosericostoma* to the Helicophidae (Flint 1979, 1983), and *Anomalopsyche* and *Contulma* placed in the new family Anomalopsychidae (Flint 1981). Four austral South American and several South African genera still remain in the Sericostomatidae, however it would not be surprising if someday they too are transferred to other notogean families.

The family Helicophidae was established by Mosely and Kimmins (1953) for the genus *Helicopha* Mosely, with two included Australian species. The genus *Alloecella* Banks, from Australia and Tasmania, was transferred to the Helicophidae by Neboiss (1977). The New Zeland genus *Zelolessica* was described by McFarlane in 1956 and *Alloecentrella* was described (Wise 1958) in the Beraeidae but later transferred to the Helicophidae (Cowley 1978). The more recent definition (Neboiss 1986) of the family has resulted in the transferral of *Alloecentrella* to the Calocidae, where it still seems quite anomalous. However, the remaining three Australasian genera are, as a result, an undoubtedly monophyletic unit.

A comparison of *Eosericostoma,* as here described, with figures and descriptions (as far as they exist) of the Australasian genera reveals the following concordances in the adult stage: antennae as long as forewing, scape elongate, but not modified otherwise; maxillary palpi 5-segmented in both sexes; a large setal wart dorsally on head, small warts behind eyes, and setal areas anteromesally; pronotum with a pair of elongate, dorsal warts; mesoscutum without warts; spurs 2,2,4; hindwing with a row of hamuli along basal portion of costal margin, with a large vein-free area in discal region. Certainly, the five-segmented maxillary palpus is plesiomorphic as is most likely the short antennae. The warts found on the head and thorax are also found in this manner in the Conoesucidae and Antipodoecidae; the Calocidae differ only in having two pairs of warts on the pronotum. This group of families are probably united in this synapomorphy, the row of hamuli on the base of the hind wing may well be another synapomorphic state. The large vein free area in the hind wing is a synapomorphy of the three Helicophid genera mentioned above.

The discordances come in the venation of the forewing primarily, although there seem to be some differences in the setation on the mesoscutellum. The latter area is shown with a pair of setate areas, or a bulging wart with lateral setate areas in the Australasian genera (Neboiss 1977, 1986). *Eosericostoma* has a setate area mesally, neither clearly divided centrally nor wart like. It would seem that *Eosericostoma* presents a further reduction in mesoscutellar warts that is already incipient in the Australasian genera and probably of no fundamental significance. The differences in forewing venation seem more profound but are hard to assess considering the great differences between the sexes and genera. If one considers only female venation, which does not suffer the specializations found in the males, a considerable agreement is seen. To start from the anterior margin: R_1 extends to the margin and is connected to R_{2+3} by a crossvein; fork 1 is present only in *Eosericostoma,* but fork 2 is present in all (accepting as inviolate the presence of the nygmal spot in fork 2 only); M is 3 branched with fork 3 present in all (the stem of M is lost in *Helicopha*); Cu_1 and Cu_2 are present, joining apicad, and with crossvein m-cu and perhaps Cu_{1b} forming an irregular anastomosis anteriad from the arculus; 1A reaches the wing margin basad of the arculus and encloses a cell basally formed from 2A and/or 3A. The discoidal cell is present and closed in *Helicopha* and *Eosericostoma,* present but open in *Alloecella,* and totally lacking in *Zelolessica* (this region is very modified in this genus and homologies are obscure).

The hindwing venation, which at first sight seems so similar in all genera, with its strange, large, open cell bearing marginal veins, actually is more perplexing to me. Possibly some of the problem lies in misrepresentation of the veins and inadvertent omission of the nygmal spot in some published figures. However the details work out in the future, it seems certain that Rs is lost in all genera, and the stem of M may also be lost in others. The situation in *Eosericostoma* is illuminating: there are two marginal veins in the male (not counting the continuation of the longitudinal veins forming the anterior and posterior margins of the cell) and the nygmal spot is lacking. In the female there are three marginal veins and the nygmal spot has appeared! This leads to the interpretation of the venation in the two sexes as labeled in Figs. 4 and 5. However, when I try to extend this interpretation through the other genera, I quickly become stymied by either too many or too few veins to complete the system. Nevertheless, I believe the basic open cell is homologous in all genera, even though it may be enlarged in a few cases by the further loss of the stem of M.

When one comes to look at homologies in the immature stages, one finds that there is very little data available. None of the Australian genera and species has been described, although they are under study (Jean Jackson, pers. comm.). Two species of the New Zealand genus *Zelolessica, cheira* (as sp.) and *meizon* (as *cheira*), are known in the larval stage and *Z. meizon* (as *cheira*) in the pupal (Cowley 1976, 1978); however the larvae and pupae were misassociated in their original description (Winterbourne & Gregson 1981, McFarlane & Cowie 1981). Considering the New Zealand species and *Eosericostoma* the larvae agree in many characteristics: head almost circular in outline, with reduced sclerotization posteriorly and ventrally; lateral constriction of frontoclypeus weak (almost lacking in *Eosericostoma*); head with primary setae only; mandibles with teeth greatly reduced, with inner hair brushes; pronotum with median, longitudinal suture and posteriorly with sclerotization reduced, with anterolateral corners rounded; legs unmodified, coxa, trochanter and femur moderately hairy; no sternal sclerites or processes; first abdominal segment with lateral humps well developed, dorsal hump reduced or lacking (*Eosericostoma*); no gills or lateral line; eighth segment with a lateral row of bifid processes; ninth segment lacking sclerotized tergite, with a few setae; anal proleg with 1 especially enlarged seta in basal tuft; anal claw with a small dorsal tooth. It seems that the primary discordances lie with: the structure of the prothoracic trochantin, elongate, acutely pointed and upturned in *Zelolessica,* elongate, nearly truncate, with a small apicodorsal tooth in *Eosericostoma*; and the mesonotum which is mostly sclerotized with a distinct mesal suture, although weakly sclerotized posteriad in *Zelolessica,* but with the sclerotization almost wholly lost except for a series of irregular patches in *Eosericostoma.*

A pupal description for *Zelolessica* is the only other knowledge of a Helicophid in this stage (Cowley 1976). There is agreement in several characteristics: antennae extended straight posteriad along body; mandibles symmetrical, long, nearly straight, base not particularly broadened, tip sharp, a row of small teeth along part, at least, of inner margin; tarsi of mid-legs with swimming fringe; abdomen with lateral fringe on segments 6–8; no gills; segment 2 with a pair of dorsal, knob like lobes bearing many spicules; hook plates anteriorly on segments 3–6, posteriorly on 5, anterior plates generally elongate with 2–4 hooks at nearly midlength, posterior plate more nearly square with 2–3 hooks posteriorly. There are two distinct differences: the tarsi of the forelegs are fringed in *Eosericostoma,* not in *Zelolessica,* and the apical process is long and slender in *Eosericostoma* but short and trucate, almost equidimensional, in *Zelolessica.*

Again, the lack of detailed information in the published descriptions for some body parts and the still unknown larvae of the other genera, makes the assessment of familial characteristics nearly impossible, and especially so for an attempt to assess which states may be synapomorphies. I consider the overall similarity in structure of body parts, warts, venation (especially that of the hindwing) of the adults to be consistent with placement of the genera *Alloecella, Eosericostoma, Helicopha* and *Zelolessica* in a single family. The differences in larval structure, especially of the mesothoracic notum, and pupal apical appendages are more difficult to reconcile within a single family, but again many other structures are concordant. In sum, I believe *Eosericostoma* is correctly placed in the Helicophidae.

I am less certain about the placement of the other Chilean genera now in the family, but there is no other family where they fit better. Perhaps another family may be recognized in the future for them, or, once all stages are well known for all the genera, a phylogenetic analysis will show them to be one or a few monophyletic lineages, resulting in different familial arrangements. For the present I leave them in the Helicophidae.

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DESIGNATION OF LECTOTYPES FOR THE SPECIES OF *MUNIDA* (CRUSTACEA: ANOMURA: GALATHEIDAE) COLLECTED BY THE U.S. COAST SURVEY STEAMER *BLAKE* (1877–1879) AND THE DESCRIPTION OF A NEW SPECIES

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Abstract.—Lectotypes of *Munida stimpsoni, M. irrasa, M. longipes, M. miles, M. microphthalma* and *M. constricta* A. Milne Edwards are designated. These species were collected by the U.S. Coast Survey Steamer *Blake* during its voyage to the Gulf of Mexico (1877–1878) and the Caribbean Sea (1878–1879). The name *Munida chacei* is proposed for a female specimen of a galatheid decapod from the syntype series of *M. stimpsoni* A. Milne Edwards, 1880, that represents a new species. The specimen, collected by the *Blake* near St. Croix, West Indies, is described and compared to *M. stimpsoni.*

Résumé.—Les lectotypes de *Munida stimpsoni, M. irrasa, M. longipes, M. miles, M. microphthalma* et *M. constricta* A. Milne Edwards sont designés. Ces espèces ont été récoltés par le *Blake* pendant ces voyages au Golfe du Mexique (1877–1878) et à la Mer des Caraibes (1878–1879). Le nom *Munida chacei* est proposé pour un spécimen femelle de galathéidés auparavant separé de la série syntipique de *M. stimpsoni.* Le spécimen récolté par le *Blake* dans les proximités de St. Croix, dans les Indes Occidentales, est décrit et comparé avec *M. stimpsoni.*

Working with part of the type material of Galatheidae of the genus *Munida* collected by the U.S. *Blake* during its cruise to the Gulf of Mexico (1877–1878) and the Caribbean Sea (1878–1879) under the supervision of Alexander Agassiz and deposited at the Harvard Museum of Comparative Zoology (MCZ) and the Muséum national d'Histoire naturelle de Paris (MNHN), we verified that the majority of the species, all described by A. Milne Edwards (1880) were represented by syntype series. Exceptions are those described from a single specimen (*M. affinis, M. robusta, M. iris* and *M. forceps*). Descriptions of the remaining species (*M. stimpsoni, M. irrasa, M. longipes, M. miles, M. microphthalma* and *M. constricta*) were based on extensive syntype series, composed of specimens from several stations. A. Milne Edwards & Bouvier (1897) described each of these species in more detailed fashion on the basis of syntypes from a single specified station. Chace (1942) examined part of this material; however, he did not designate lectotypes. These are selected herein among the syntypes described by A. Milne Edwards & Bouvier. A diagnosis and measurements (mm) are provided for each lectotype.

Chase verified the existence of several other species in the syntype series of *M. stimpsoni* and described some of these. From this series we separated an ovigerous female, with label: "MCZ-11527, Syntype, *Munida stimpsoni* A. Milne Edwards, 1880; 1 ovig. female, *Blake* st. 134, 248 fms., off Saint Croix, 1878–79. Identified as *Munida* sp.n. by Chace." Comparing this specimen with types of the remaining species from the Western Atlantic, it became clear that it was an undescribed species.

Munida stimpsoni A. Milne Edwards, 1880

Munida Stimpsoni A. Milne Edwards, 1880: 47 (part).—A. Milne Edwards & Bouvier, 1897:48 (part), pl. IV, figs. 2–13 (not fig. 1).

Munida stimpsoni.—Chace, 1942:57, text-fig. 23a, b.

Lectotype.—♂, MCZ 2825, *Blake* st. 143, Saba Bank, 17°30′00″N, 68°43′30″W, 270 m.

Measurements (mm).—Length of carapace + rostrum 12.1; rostrum length 4.4; carapace breadth 6.5; supra-ocular spines length 2.3; cornea diameter 2.5; chelipeds: lacking.

Diagnosis.—Lateral borders of carapace subparallel. Outer orbital spines followed by 3 lateral spines. Gastric area with 6 spines: 1 pair behind supra-oculars, followed by 1 smaller pair; 1 single median spine in line with rostrum, and 1 spine at division with right hepatic area, corresponding area on left side without spine. Anterior branchial areas with 1 spine. One strong post-cervical spine on each side. Cardiac area with median spine. Rostrum projecting horizontally. Supra-ocular spines long, slightly divergent. Eyes with rounded corneas, broader than peduncles. Abdominal tergite 2 with 8 (3-2-3), tergite 3 with 4 (1-2-1), and tergite 4 with 6 (2-2-2) spines on anterior ridge and 1 median posterior spine, forming triangle with 2 anterior submedian spines. Peduncle of antennule with inner spine little larger than outer spine, and with lateral margin with distal spine longer than proximal spine. Segment 2 of peduncle of antenna distally with small outer spinule and 1 inner spine. Third maxilliped with strong spine on ventral margin of merus.

Remarks.—According to Chace (1942) the syntype series of *M. stimpsoni* is composed of several species in addition to *M. stimpsoni*; these are *M. benedicti* Chace (*Blake* st. 143, 203 and 231); *M. evermanni* Benedict (*Blake* st. 148, 206, 219, and 238); *M. flinti* Benedict (*Blake* st. 36 and 262); *M. miles* A. Milne Edwards (*Blake* st. 148 and 215); *M. striata* Chace (*Blake* st. 128, 134 and 139); and a *Munida* n.sp. (*Blake* st. 134), identified by Chace as a new species and described herein.

The specimen from *Blake* st. 36, *M. flinti,* according to Chace (1942) was used by A. Milne Edwards & Bouvier (1897: pl. IV, fig. 1) to illustrate *M. stimpsoni.*

Munida benedicti, M. striata and *M. flinti* are very similar to *M. stimpsoni.* In addition to the differences listed by Chace (1942) between *M. stimpsoni* and *M. flinti,* the distal spines of the second antennal segment in *M. stimpsoni,* are absent or much reduced in *M. flinti,* as indicated by the syntypes of the latter (U.S. National Museum of Natural History, USNM 5778) as well as by the specimens from *Blake* st. 262. In spite of the fact that A. Milne Edwards & Bouvier (1897) compared *M. stimpsoni* with *M. longipes,* there is apparently no close relationship between these two species.

Among the many stations cited by A. Milne Edwards (1880) and A. Milne Edwards & Bouvier (1897), from which the syntype series of *M. stimpsoni* originated, only at stations 23 (off the north coast of Cuba); 128 (off St. Croix); 143 (off Saba Bank); 148 (off St. Kitts); 167, 172 (off Guadaloupe); 184, 186 (off Dominica); and 238 (off Grenadines), were true *M. stimpsoni* obtained (Chace 1942).

Note also that the coordinates furnished by A. Milne Edwards & Bouvier (1897) for *Blake* st. 143 (17°30′N, 69°43′½″W) are not confirmed by the tag which accompanies the specimen (17°30′00″N, 63°43′30″W).

Munida irrasa A. Milne Edwards, 1880

Munida caribaea Stimpson, 1860:246.—A. Milne Edwards & Bouvier, 1897:25, pl. I, figs. 16–20, pl. II, fig. 1.

Munida irrasa A. Milne Edwards, 1880: 49.—Faxon, 1895:73.—Chace, 1942:46.
Munida cariboea A. Milne Edwards, 1880: 49.
Munida caribea.—Türkay, 1968:249.

Lectotype.—♀, MCZ 4714, *Blake* st. 253, off Grenada, 1878–1879, 165 m.

Measurements (mm).—Length of carapace + rostrum 14.1; rostrum length 5.3; carapace breadth 7.8; cornea diameter 2.3; supra-ocular spines length 0.8; right cheliped: length 34.9, length of dactyl and fixed finger 8.2, palm length 8.1, palm height 1.7; left cheliped: lacking.

Diagnosis.—Lateral borders of carapace arcuate. Outer orbital spine followed by 6 lateral spines. Gastric line with 9 spines: 1 large gastric pair behind supra-oculars, 3 spines on left side and 4 on right side. One pair of para-hepatic spines on each side of carapace. Anterior branchial regions with 2 spines. Two post-cervical spines on each side of carapace. Rostrum with tip upturned. Supra-ocular spines short. Eyes with rounded corneas, broader than peduncles. Abdominal tergites without ornament. Peduncle of antennule with inner terminal spine much longer than outer terminal spine. Peduncle of antenna with 2 spines on segment 2, outer distal spine longer. Segment 3 with outer distal denticle and 1 small inner distal spine. Merus of third maxilliped with 3 spines on dorsal margin and 4 or 5 spines on ventral margin. Sternite of third maxilliped with upper margin spinous. Sternites of chelipeds with crenulate margins and strong spine on each antero-lateral angle.

Remarks.—A. Milne Edwards & Bouvier (1897) considered *M. irrasa* a junior synonym of *M. caribaea* Stimpson, 1860. Thus, the syntypes of *M. irrasa* collected by the *Blake,* especially those of st. 253, were utilized by the former authors in a detailed description of *M. caribaea.* Nevertheless, the opinion of Faxon (1895), that *M. caribaea* should be suppressed in favor of *M. irrasa,* because of the destruction of the types of the former species and the insufficiency of the description of Stimpson (1860), was supported by Benedict (1902) and by Chace (1942). *M. irrasa* is closely related to *M. elfina* Boone, *M. sculpta* Benedict, and *M. simplex* Benedict.

MCZ lot 4714 from *Blake* st. 253 consists of two females, one of these ovigerous. The latter specimen being incomplete, the lectotype selected is the former, non-ovigerous female.

Munida longipes A. Milne Edwards, 1880

Munida longipes A. Milne Edwards, 1880: 50.—A. Milne Edwards & Bouvier, 1897: 44, pl. III, figs. 9–13.—Chace, 1942:47.

Lectotype.—Ovigerous ♀, MNHN Ga 543, *Blake* st. 274, off Barbados, 376 m.

Measurements (mm).—Length of carapace + rostrum 19.4; rostrum length 3.9; carapace breadth 14.6; supra-ocular spines length 4.0; right cheliped (broken): length of merus 23.3, palm length 14.1, palm height 2.2; left cheliped: lacking, length of merus of 1st ambulatory leg 25.6.

Diagnosis.—Lateral borders of carapace arcuate. Outer orbital spine followed by 5 lateral spines. Gastric area with 3 spines: 1 pair of strong spines behind supra-oculars and 1 para-hepatic spine on right side, left side lacking spine. Anterior branchial areas without ornament; posterior branchial areas with 1 spine aligned with post-cervical spine. Cardiac area with 1 central spine above meso-cardiac groove. Posterior margin of carapace with 1 pair of spines. Rostrum short, upturned. Supra-ocular spines strong, divergent, length equal to length of rostrum. Eyes with rounded corneas, broader than peduncles and ciliated. Abdominal tergites 2 and 3 each with 4 spines on anterior margin; tergite 4 with only 1 pair of spines. Peduncle of antennule with inner terminal spine much smaller than outer terminal spine. Peduncle of antenna with 2 small spines on second segment. Third maxilliped with 1 strong spine on ventral margin. Sternum without ornament, rugose. Ambulatory legs characteristically long, length equal to length of cheliped.

Remarks.—Chace (1942) synonymized *Munida paynei* Boone with *M. longipes.* Although Boone (1927) had listed several differences between the two species, Chace concluded that *M. paynei* is within the gradient of variation of *M. longipes.*

Munida miles A. Milne Edwards, 1880

Munida miles A. Milne Edwards, 1880:51 (part).—A. Milne Edwards & Bouvier, 1897:35 (part).—Chace, 1942:36 (part).
Munida decora Benedict, 1902:257.
Not *M. miles.*—Henderson, 1888:126 (see Remarks).

Lectotype.—♂, MCZ 4728, *Blake* st. 274, off Barbados, 1878–1879, 376 m.

Measurements (mm).—Length of carapace + rostrum 23.9; rostrum length 6.0; carapace breadth 14.9; cornea diameter 3.4; supra-ocular spines length 2.0; right cheliped: length 59.8, length of dactyl and fixed finger 13.5, palm length 14.1, palm height 6.0; left cheliped: length 57.8, length of dactyl and fixed finger 13.2, palm length 13.4, palm height 6.7.

Diagnosis.—Lateral borders of carapace arcuate. Outer orbital spines on frontal margin of carapace followed by 6 lateral spines. Gastric area with 8 spines: 5 spines on left side and 3 on right side, including 1 pair of small spines between pair of large median spines. One para-hepatic spine on either side of carapace. Remainder of carapace without ornament. Rostrum upturned. Supra-ocular spines short and divergent. Eyes with rounded corneas, broader than peduncles. Abdominal tergite 2 with a row of 8 spines on anterior ridge. Tergite 3 with 1 pair of median spines. Tergite 4 without spines. Peduncle of antennule with outer terminal spine longer than inner spine. Peduncle of antenna with 1 distomesial spine on segment 1, and 1 distomesial and 1 distolateral spine on segment 2. Merus of third maxilliped with 2 spines on ventral margin and 1 little tubercle between them. Sternum smooth and without ornament, sternites with crenulate margins.

Remarks.—The MCZ lot 4728 contains two males. It seems that A. Milne Edwards & Bouvier (1897) described and measured the specimen bearing unequal chelipeds, the left one clearly smaller; however, this specimen is incomplete since it is broken at the fourth abdominal tergite. Thus, the lectotype chosen is the other male, in which the chelipeds have about the same length. According to Chace (1942) the specimens from *Blake* st.11 (1 male and 1 female syntypes of *M. miles*) plus one female from st. 45 and another female from st. 232, should be referred to *M. nuda,* a much smaller species. This author considered *M. decora* Benedict synonymous with *M. miles* and mentioned the latter from *Blake* st. 45, 53, 129, 146, 147, 148, 153, 154, 209, 215, 218, 232, 241, 275 and from off Grenada (unknown station). We have examined specimens from *Blake* st. 148 (1 male, MNHN Ga 545), 218 (1 male with parasite, MNHN Ga 546) and 215 (1 ovigerous female, MCZ 2826, syntype of *M. stimpsoni,* actually *M. sanctipauli* Henderson). Based on the poor description of *M. miles* given by A. Milne Edwards (1880), Henderson (1888) considered it synonymous with *M. valida* Smith, but we think they are different species. Reexamination of the *Challenger* material is under way and will resolve this question.

Munida microphthalma
A. Milne Edwards, 1880

Munida microphthalma A. Milne Edwards, 1880:51 (part).—A. Milne Edwards & Bouvier, 1897:32, pl. II, figs. 9–13.—Chace, 1942:40, text-fig. 16.

Lectotype.—♂, MCZ 4727, *Blake* st. 227, off St. Vincent, 1878–1879, 1031 m.

Measurements (mm).—Length of carapace + rostrum 21.7; rostrum length 7.3; carapace breadth 11.2; cornea diameter 1.6; supra-ocular spines length 2.5; right cheliped: length 36.5, length of dactyl and fixed finger 8.8, palm length 8.5, palm height 3.9; left cheliped: lacking.

Diagnosis.—Lateral borders of carapace arcuate. Outer orbital spine on frontal margin of carapace, followed by 6 strong lateral spines. Gastric area with row of 6 spines. Remainder of carapace unarmed. Rostrum distinctly upturned. Supra-ocular spines divergent, slightly exceeding cornea. Eyes characteristically small, cornea scarcely broader than stalk. Abdominal tergite 2 with row of spines on anterior ridge. Tergites 3 and 4 unarmed. Peduncle of antennule with outer terminal spine much longer than inner spine. Segment 1 of peduncle of antenna with 1 inner spine; segment 2 distally with 1 inner spine and 1 outer spine; and segment 3 with 1 inner terminal spine. Merus of third maxilliped with 2 spines on ventral margin and 2 tubercles between them. Sternum without ornament except for fine granulation on sternites of third ambulatory legs.

Remarks.—*Munida microphthalma* is very similar to *M. microps* Alcock, *M. perlata* Benedict and *M. subcaeca* Bouvier. *M. microps* is larger and has post-cervical and anterior branchial spines. *M. perlata* has shorter supra-ocular spines and only one spine on the ventral margin of the merus of the third maxilliped. *M. subcaeca* is smaller and presents external orbital spines reduced and abdominal tergites unarmed.

Chace (1942) was aware that the male specimen from *Blake* st. 2 (Morro Castle, Cuba, 1450 m, syntype of *M. microphthalma*) and the male from st. 131 (St. Croix, 1044 m) should actually be considered *M. subcaeca.*

Except for its reduced cornea, *M. microphthalma* is similar to *M. sanctipauli* as it became evident when the type-series of both species were compared. Bouvier (1922) had already noted this similarity: "L' espèce me parait très voisine du *M. Sancti-Pauli,* elle n'en diffère que par ses yeux rèduits . . . Dès lors, le *M. microphthalma* serait une simple variété du *M. Sancti-Pauli.* Des recherches ultérieures jetteront certainement de la lumière sur ce point." We prefer to consider both species distinct until the relative diameter of the cornea can be better evaluated as a character.

Munida constricta
A. Milne Edwards, 1880

Munida constricta A. Milne Edwards, 1880: 52 (part).—A. Milne Edwards & Bouvier, 1897:40, pl. III, fig. 5.—Chace, 1942:34, text-figs. 14a, b.

Lectotype.—♂, MNHN Ga 534, *Blake* st. 221, St. Lucie, 13°53′N, 60°58′W, 760 m.

Measurements (mm).—Length of carapace + rostrum 15.7; rostrum length 5.0; carapace breadth 7.6; supra-ocular spines length 2.0; cornea diameter 2.5; right cheliped (only chela): length of dactyl and fixed finger 6.5, palm length 5.9, palm height 2.6; left cheliped (only chela): length of dactyl and fixed finger 6.5, palm length 6.5, palm height 2.6.

Diagnosis.—Lateral borders of carapace parallel. Outer orbital spine followed by 6 lateral spines. Gastric line with 8 spines, including 1 pair of small spines between pair of large medial spines. Strong para-hepatic spine on margin of anteriormost continuous transverse line. Remainder of carapace without ornament. Rostrum long, distal extremity upturned. Supra-ocular spines short and slightly divergent. Abdominal tergite 2 with 7 spines on anterior margin. Tergite 3 with 1 pair of strong central spines and 1 denticle on each side. Tergite 4 with 1 pair of median spines. Peduncle of antennule with outer terminal spine longer than inner spine and with outer dorso-lateral spine followed by 1 smaller proximal outer lateral spine. Peduncle of antenna with 1 long distomesial spine on segment 1 and 1 distolateral denticle on segment 2. Third maxilliped with 1 long proximal spine and 1 shorter distal spine. Sternum smooth, without ornament.

Remarks.—According to Chace (1942) there exists a female of this species at the MCZ, collected at *Blake* st. 230, off St. Vincent, not mentioned by A. Milne Edwards & Bouvier (1897). Two lots of the syntype series, however, from St. Kitts (st. 146 and 147) are *M. miles.* The difficulty in separating *M. constricta* from *M. miles* was noted by A. Milne Edwards & Bouvier (1897: 41): ". . . les différences qui séparent la *M. miles* de la *M. constricta* ne nous paraissant pas irréductibles, mais les termes de passage entre les deux espèces faisant jusq'ici complétement défaut, il est necessaire de les séparer l'une de l'autre en attendant des recherches nouvelles."

Munida chacei, new species
(Figs. 1–7)

Munida stimpsoni.—A. Milne Edwards, 1880:47 (part).—A. Milne Edwards & Bouvier, 1897:52 (part).

Material examined.—Holotype: 1 ovigerous ♀ (MCZ 11527), *Blake* st. 134, off Saint Croix, West Indies, 17°54′N, 64°45′W, 1878–1879, 446 m.

Diagnosis.—Lateral margins of carapace with 3 spines. Gastric area with longitudinal row of 6 spines, aligned with rostrum; 3 pairs of gastric spines behind supra-oculars. One pair of spines outside line of supra-oculars, near second gastric spine pair. One para-hepatic and 2 hepatic spines on each side. Right anterior branchial region with 1 spine, left with 2 spines. Two pairs of post-cervical spines and 1 cardiac spine. Two spines on intestinal region. Posterior margin of carapace with 2 pairs of spines. Second abdominal tergite with 8 (2-2-2-2) and third tergite with 4 (1-2-1) spines. Antennular peduncle with inner terminal spine longer than outer. Merus of third maxilliped with 1 ventral spine. Sternum unarmed, smooth.

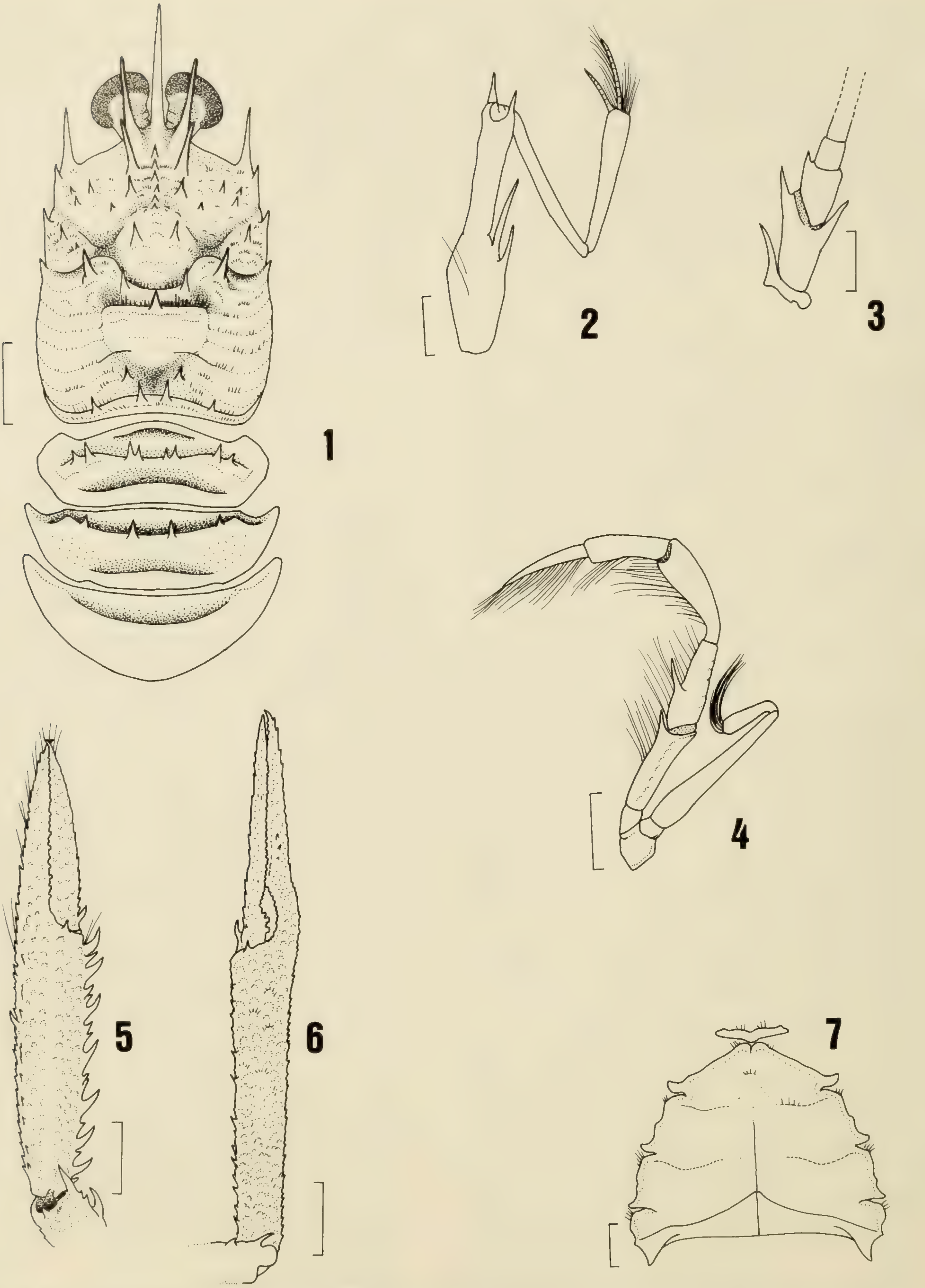
Description.—Carapace slightly longer than broad. Greatest breadth at level of meso-cardiac groove. Outer orbital spines long, overreaching corneas, followed by 3 lateral spines: 1 above lateral angle of carapace, 1 on anterior margin of branchial region, and 1 slightly behind posterior branch of cervical groove, this last spine smaller than preceding 2 and located more ventrally. Gastric area with longitudinal row of 6 small spines in line with rostrum, 3 pairs of large spines behind supra-oculars: first pair epigastric, extremely long, equal to outer orbital, curved upwards and forwards, at same angle as supra-oculars; middle pair proto-gastric, much smaller than anterior pair; and 1 metagastric pair, smallest and set more closely together than preceding pair. One pair of small spines postero-lateral to proto-gastric pair. One para-hepatic and 2 hepatic pairs of spines on each side. Anterior branchial region with 2 spines on left side and 1 spine on right side. Four strong post-cervical spines: 1 inner pair, behind proto-gastric pair, and 1 outer pair, proximal to branching of cervical groove. Cardiac region with 1 spine above meso-cardiac groove. Intestinal region with 1 pair of spines. Posterior margin of carapace with 4 spines.

Rostrum directed forwards and upwards, distal third with indistinct serrations on upper surface. Supra-ocular spines long, divergent, directed upwards and slightly sinuous.

Eyes with rounded corneas, broader than peduncles which have naked margins.

Second and third abdominal tergites armed with 8 (2-2-2-2) and 4 (1-2-1) spines respectively, both with broad central ciliated groove. Fourth and fifth tergites unarmed and smooth.

Basal segment of antennular peduncle with distal half elongate and with 2 distal spines, inner spine slightly longer than outer. Prox-



Figs. 1–7. *Munida chacei,* new species. Holotype ovigerous female: 1, carapace and abdominal somites 2–4, dorsal view; 2, antennular peduncle; 3, antennal peduncle; 4, third maxilliped; 5, left chela, dorsal view; 6, right chela, dorsal view; 7, sternum. Scales equal 3 mm (1, 6), 1 mm (2, 3, 7), 5 mm (4), and 4 mm (5).

Table 1.—Characters that differentiate *M. chacei*, new species, from *M. stimpsoni* A. Milne Edwards.

	M. chacei	*M. stimpsoni*
Gastric spines aligned with rostrum	6	0
Spines on metagastric region	2 lateral	1 central
Post-cervical spines	4	2
Spines on posterior margin	4 (1-2-1)	2
Spines on intestinal region	2	0
Spines on 2nd abdominal tergite	8 (2-2-2-2)	8 (3-2-3)
Spines on 3rd abdominal tergite	4 (1-2-1)	6 (2-2-2)
Spines on antenna segment 3	1 (inner border)	0
Sternum	smooth	wholly rugose
Coxa of cheliped	spinous	smooth
Pleura of abdominal somites	somites 4 acute, others rounded	somite 2 rounded, others acute

imal half with 1 long dorsolateral spine curved longer than outer. Proximal half with 1 long dorsolateral spine curved upwardly, and 1 spine proximal to first spine, strong but shorter than first spine.

Basal segment of peduncle of antenna with long inner distal spine. Second segment of antenna with strong inner distal spine and another outer distal spine. Third segment with 1 small inner distal spine.

Third maxilliped with dorsal inner margin of ischium denticulate. Ischium with 1 distal spine on ventral margin. Ventral margin of merus with 1 long median spine. Hair-bearing line extending from ischium to dactylus.

Chelipeds scaly, sparsely hairy. Left cheliped more robust, with carpus bearing 3 rows of spines in addition to terminal spine: 1 row on each margin, excepting unarmed lower mesial margin. Palm with rows of strong spines on mesial surface, some spines on dorsal lower surface and 2 small spines on ventral and dorsal sides near articulation with movable finger. Movable finger with row of spinules on mesial surface. Entire cutting surfaces of both fingers denticulate. Fingers each with curved terminal spine crossing at tips. Right cheliped more slender than left. Carpus with row of spinules on dorsal lateral margin and some spinules near articulation with chela. Palm elongate, with row of spinules on dorsal mesial margin. Fixed finger with proximal hiatus on cutting surface and subterminal spines on lateral surface. Movable finger with 2 proximal molars on cutting surface and mesial surface with only 2 subterminal spines. Cutting surface denticulate between hiatus and distal end.

Ambulatory legs laterally compressed, sparsely haired. Merus with 2 rows of strong, forwardly-curved spines on dorsal and ventral surfaces, including long terminal spine. Carpus with row of spines on dorsal and ventral surfaces, and 1 terminal spine on each surface. Propodus and dactylus each with rows of movable spines on ventral surface.

Sternum smooth, without spines. Sternite of third maxilliped with upper and lateral margins denticulate. Dividing lines of sternites finely granulate.

Measurements of holotype (mm).—Carapace length excluding rostrum 10.9; carapace breadth 9.2; rostrum length (point broken) 5.7; supra-ocular spines length 3.3; cornea diameter 2.6; right cheliped: length of dactyl and fixed finger 9.4, palm length 13.6, palm height 2.1; left cheliped: length of dactyl and fixed finger 12.2, palm length 13.6, palm height 2.1.

Type locality.—Near St. Croix, West Indies, 17°54′N, 64°45′W, 446 m.

Etymology.—This species is dedicated to Dr. Fenner A. Chace, Jr., in recognition of his great contributions to carcinology and of his first indication that this species was new to science.

Remarks.—Similarities exist between *M. chacei* and *M. stimpsoni.* Characters that differentiate the two species are summarized in Table 1.

Acknowledgments

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LARVAL DEVELOPMENT OF THE GOLDEN CRAB, *CHACEON FENNERI* (MANNING & HOLTHUIS, 1984) (DECAPODA: BRACHYURA: GERYONIDAE), REARED IN THE LABORATORY

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Abstract.—Several thousand first stage zoeae were isolated from a holding tank containing ovigerous females of *Chaceon fenneri* collected from slope waters west of Tampa Bay, Florida. Larvae were reared individually and in mass cultures at 18°C and 30 ppt salinity. Four zoeal stages and a megalopal stage obtained from the mass cultures are described and illustrated. Comparisons are made with previously described larvae of *Geryon tridens* from the eastern North Atlantic, *Chaceon quinquedens* from the western North Atlantic, and *C. quinquedens* from the Gulf of Mexico, the latter also cultured during the present study. Zoeae of *C. fenneri* lack dorsolateral spines on the fifth abdominal segment, allowing them to be easily distinguished from zoeae of it's congener, *C. quinquedens.* Megalopae of *C. fenneri* and *C. quinquedens* can be distinguished by the number of long, hooked setae on the dactyl of the fifth pereiopod. Characters distinguishing larvae of *C. fenneri* from morphologically similar non-geryonid larvae found in the northern Gulf of Mexico are presented.

Deep water crabs of the family Geryonidae are widely distributed throughout the world oceans. The family was revised by Manning & Holthuis (1989) to include three genera and 24 species. The authors restricted the genus *Geryon* Kröyer to two species, *G. longipes* A. Milne Edwards and *G. trispinosus* (Herbst), both from the northeastern Atlantic Ocean. The genus *Chaceon* Manning & Holthuis contains the majority of the known geryonids, with 21 species described. Species of *Chaceon* form the basis of deep water fisheries along both sides of the Atlantic.

Two species of *Chaceon* were identified by Perry et al. (1989) and Lockhart et al. (1990) from trapping surveys of the eastern and central Gulf of Mexico: *C. quinquedens* (Smith) and *C. fenneri* (Manning & Holthuis). Though some overlap in geographic and depth distribution was reported in these studies, the species are essentially separated geographically and bathymetrically. *Chaceon fenneri* is restricted to the upper continental slope off peninsular Florida and predominates at depths of 311 to 494 m; *Chaceon quinquedens* is abundant at depths of 677 m and below. During the course of the 1988 winter trapping survey (Lockhart et al. 1990), ovigerous females of both species were collected and the larvae reared. The present study describes the complete larval development of *C. fenneri,* and provides comparisons with zoeae of *C. quinquedens* as described by Perkins (1973) and zoeae of *C. quinquedens* reared from Gulf of Mexico specimens. Characters allowing separation of geryonid larvae from the larvae of *Ovalipes floridanus* Hay & Shore, *Menippe mercenaria* (Say), and *Menippe adina* Williams & Felder, are discussed.

Methods

Ovigerous females of *C. fenneri* were collected from slope waters of 311 m depth west of Tampa Bay, Florida (27°03′52″N, 84°49′08″W), and maintained in refrigerated seawater systems at 11°C. Several hundred first zoeae were recovered from one of the systems on February 28, 1988. The larvae were immediately returned to the laboratory and separated into eight four-inch culture bowls. Fifteen larvae were placed individually into two-inch culture bowls.

Larvae of *C. quinquedens* were obtained by removing late stage eggs from ovigerous females held in the laboratory at 11°C and gradually increasing the temperature by 3°C per day. These eggs normally hatched within four days of isolation, and the larvae were mass cultured in four-inch culture bowls. No individual cultures were attempted.

Larvae of both geryonids were cultured in filtered deionized water containing 32 ppt salt (hw-Marinemix) to which 50 mg/l streptomycin sulfate and 40 mg/l penicillin had been added. Cultures were incubated at 18°C with a 12-h photoperiod. Larvae were fed daily a mixture of rotifers (*Brachionus plicatilis*) packed with the diatom *Chaetocerous gracilis* and freshly hatched brine shrimp (*Artemia*). Every two days the water in all bowls was changed and exuviae, dead larvae, and several live specimens were removed from the mass cultures, initially preserved in 5% buffered formalin, and later transferred to 70% ethanol. Individually held larvae were checked daily for the presence of molts. At least 10 specimens obtained from the mass cultures were measured and dissected for each stage, zoea I through megalopa, using the procedures outlined by Stuck and Truesdale (1988). Drawings and measurements were made with the aid of a camera lucida. A developmental series of zoea I through megalopa was deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 244325).

Results

Prezoeae of *Chaceon quinquedens* were observed just after hatching of some incubated eggs, but rarely developed into viable first zoeae. *C. fenneri* were recovered from holding tanks as a first zoea, therefore it is unknown if a prezoeal stage was present.

All individually held larvae of *C. fenneri* died before or during the molt to zoea III. Most larvae held in mass cultures completed development through megalopae in 33–40 days. Four distinct zoeal stages and a megalopal stage were recovered from the mass cultures. None of the megalopae successfully completed metamorphosis to a viable first crab stage. Some fourth stage zoeae appeared to enter a fifth zoeal stage characterized by additional setae and spines on the maxilla, maxillule, maxillipeds, and extensive development of pereiopod buds. However, since individually held larvae did not survive beyond zoeae III, there is no direct evidence for the existence of a fifth zoeal stage. Cursory observations on pigmentation of larval *C. fenneri* made from live specimens indicated chromatophore patterns similar to those described for *C. quinquedens* by Perkins (1973). The intensity of the pigmentation appeared to be highly variable between individuals. Setae types on the appendages of the zoeae and megalopa of *C. fenneri* are similar to those illustrated by Stuck & Truesdale (1988) for *Arenaeus cribrarius* Lamarck.

Description of developmental stages.—Morphometrics for the zoeal and megalopal stages of *C. fenneri* are given in Table 1.

Zoea I

Carapace (Fig. 1A).—With dorsal spine well developed, long and slender, straight to slightly recurved; rostral spine straight; lateral spines long; dorso-medial ridge present anterior to dorsal spine; pair of short simple setae present near base of dorsal spine; posterolateral margin of carapace finely serrate. Eyes sessile.

Antennule (Fig. 1B).—Unsegmented, with 2 terminal aesthetascs, 2 setae of unequal length and 1 minute setule.

Antenna (Fig. 1C).—Protopodite long,

Table 1.—Morphometrics (mean, standard deviation, and range) of zoeal and megalopal stages of *Chaceon fenneri* (measurements in mm). Measurements were made following procedures outlined by Stuck & Truesdale (1988). Total length: anterior margin of the carapace at orbit to posterior tip of telson; total spine length: tip of dorsal spine to tip of rostral spine; rostral length: anterior margin of orbit to tip of rostral spine; dorsal spine length: dorsal margin of carapace to tip of dorsal spine; carapace spine width: distance between tips of carapace spines; carapace length: anterior margin of carapace at orbit to posterior carapace border.

Stage	No.	Total length	Total spine length	Rostral length	Dorsal spine length	Carapace/ spine width	Carapace length
Zoea I	10	2.83 ± 0.17 (2.65–3.01)	2.63 ± 0.14 (2.50–2.86)	0.71 ± 0.06 (0.60–0.80)	1.08 ± 0.04 (1.05–1.15)	1.55 ± 0.08 (1.55–1.78)	1.02 ± 0.04 (0.95–1.08)
Zoea II	10	3.42 ± 0.24 (3.11–3.72)	3.41 ± 0.20 (3.01–3.62)	0.94 ± 0.12 (0.85–1.05)	1.38 ± 0.16 (1.20–1.62)	1.97 ± 0.12 (1.80–2.18)	1.20 ± 0.09 (1.10–1.37)
Zoea III	10	4.69 ± 0.22 (4.28–5.00)	4.36 ± 0.20 (4.03–4.59)	1.26 ± 0.11 (1.08–1.40)	1.77 ± 0.14 (1.56–1.95)	2.64 ± 0.08 (2.50–2.75)	1.58 ± 0.10 (1.45–1.78)
Zoea IV	10	5.76 ± 0.40 (5.41–6.53)	5.78 ± 0.38 (5.00–6.32)	1.52 ± 0.25 (1.15–1.95)	2.31 ± 0.19 (2.04–2.70)	3.29 ± 0.19 (2.96–3.57)	2.34 ± 0.17 (2.04–2.50)
Megalopa	10	5.59 ± 0.27 (5.30–5.90)				2.91 ± 0.18 (2.65–3.06)	3.26 ± 0.29 (3.15–3.40)

with rows of spines on distal half; spinous process approximately ⅔ length of rostral spine; length of exopod half length of protopod, terminating in 1 long and 1 short simple seta.

Mandible (Fig. 1D).—With incisor and molar processes well developed, palp absent.

Maxillule (Fig 1E).—Endopod 2-segmented, distal segment with 4 long terminal and 2 subterminal plumose setae, proximal segment with long plumose seta, setation pattern unchanged through zoea IV; basial endite with 3 marginal and 3 submarginal setae (types as illustrated); coxal segment with 1 submarginal and 6–7 marginal setae.

Maxilla (Fig. 1F).—Scaphognathite with 6–8 plumose setae, distal end produced into slender plumose tip; endopod bilobed, distal lobe with 5 marginal setae, proximal lobe with 1 submarginal and 2 marginal setae (types as illustrated), setation pattern unchanged in succeeding zoeal stages; basial endite bilobed, distal lobe with 1 submarginal and 4 marginal setae, proximal lobe with 1 submarginal and 3 marginal setae; distal lobe of coxal endite with 1 marginal, 1 short and 2 long submarginal setae, proximal lobe with 1 marginal and 2 submarginal setae.

Maxilliped 1 (Fig. 1G).—Coxa with 1 lateral plumose seta; basis bearing 10 sparsely plumose setae clustered in proximal to distal groups of 2, 2, 3, and 3, unchanged in succeeding zoeal stages; endopod 5-segmented, with proximal to distal setation pattern of 2, 2, 1, 2, 4 and 1 subterminal sparsely plumose setae; exopod unsegmented, bearing 4 long natatory setae.

Maxilliped 2 (Fig. 1H).—Coxa lacking setae; basis bearing 4 sparsely plumose setae; endopodite 3-segmented, distal margin of proximal 2 segments each with 1 sparsely plumose seta, distal segment with 5 marginal plumose setae of different lengths and 1 minute submarginal simple seta; coxa, basis, and endopod unchanged in succeeding zoeal stages; exopod incompletely segmented, bearing 4 long natatory setae.

Abdomen (Fig. 1A, I).—Five-segmented, dorsolateral surface of segment 2 with pair of blunt anteriorly pointing spines, segment 3 with smaller pair of posteriorly pointing spines, segment 4 with pair of minute laterally projecting spines; segments 3–5 with acute posterolateral projections, decreasing

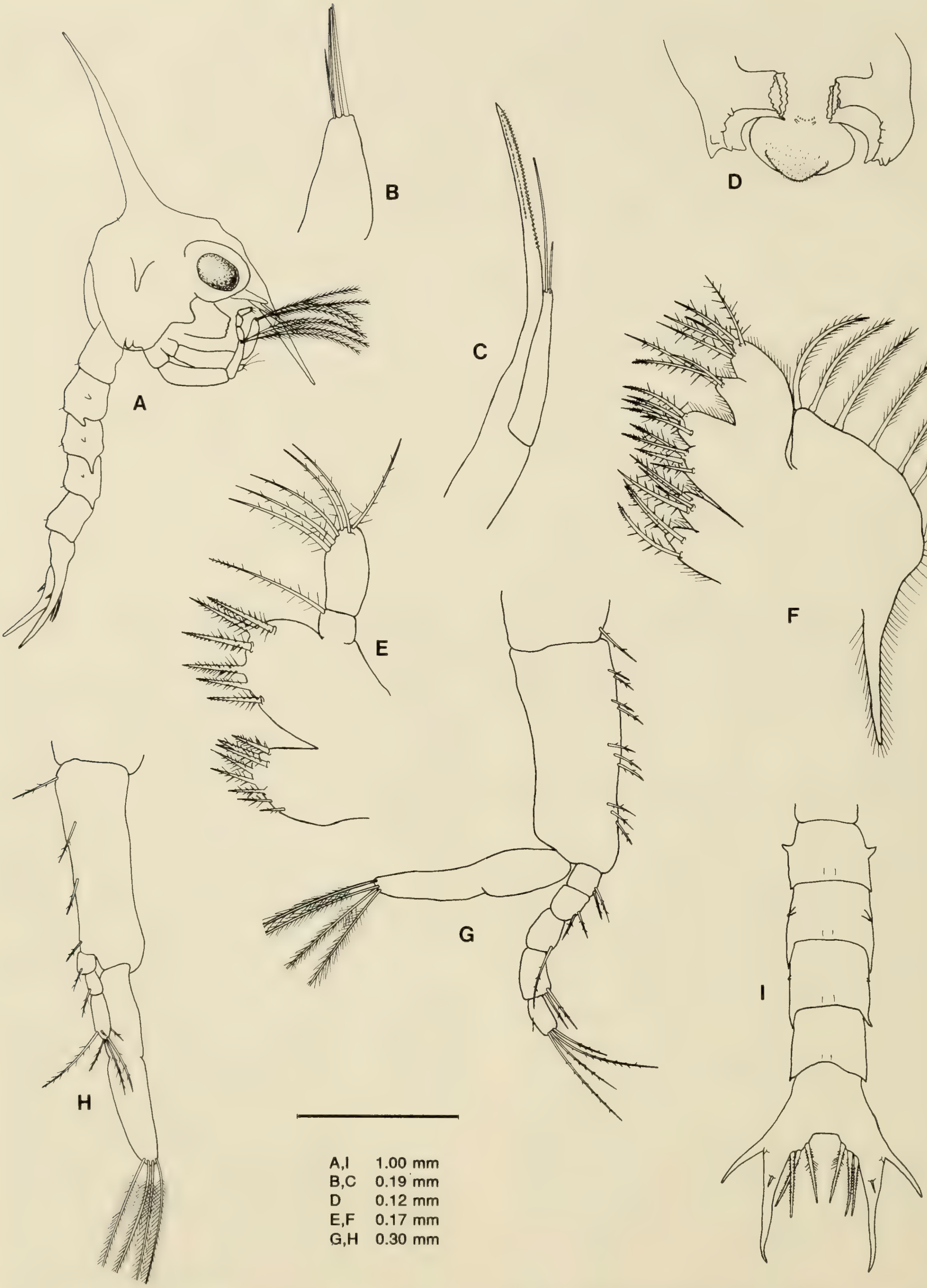


Fig. 1. *Chaceon fenneri* Manning & Holthuis. First zoea: A, Lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped 1; H, Maxilliped 2; I, Abdomen and telson (dorsal view).

in length from anterior to posterior, segments 2–5 each with pair of minute dorsal setae.

Telson (Fig. 1I).—Furcate, each ramus bearing 1 strong and 1 minute lateral spine, and 1 small dorsal spine; posterior margin of telson bearing 3 pairs of large serrate spines, innermost seta armed medially with stiff setules.

Zoea II

Carapace (Fig. 2A).—With pair of setae present anterior to dorsal spine, posterolateral margins of carapace with 4–5 setae, otherwise carapace as in zoea I. Eyes stalked. Small pereiopod buds visible beneath carapace.

Antennule (Fig. 2B).—Bearing 5 aesthetascs, 1–2 short simple setae, and 1 setule.

Antenna (Fig. 2C).—With long terminal setae of exopod reaching to tip of protopod, spinous process slightly greater than half length of rostrum; endopod bud present, otherwise similar to zoea I.

Maxillule (Fig. 2D).—With large plumose seta added below base of endopod, present in all succeeding zoeal stages; basial endite with 5 stout and 2 slender marginal setae and 4 submarginal setae; coxal endite with 7 marginal and 3 submarginal setae.

Maxilla (Fig. 2E).—Scaphognathite with 13–18 plumose setae; distal lobe of basial endite with 1 submarginal and 5 marginal setae, proximal lobe with 3–4 marginal and 2 submarginal setae; distal lobe of coxal endite with 1 marginal and 3 submarginal setae, proximal lobe with 2 marginal and 3–4 submarginal setae.

Maxilliped 1 (Fig. 2F).—Coxa with 1 lateral plumose seta; endopod with proximal to distal setation pattern of 2, 2 (rarely 3), 1 (rarely 2), 2, 4 and 1 subterminal sparsely plumose seta; exopod 2-segmented, bearing 10 natatory setae.

Maxilliped 2 (Fig. 2G).—Exopod bearing 10–11 natatory setae.

Telson (Fig. 2H).—Posterior margin bearing medial pair of small serrate spines between larger spines, otherwise similar to zoea I.

Zoea III

Carapace (Fig. 3A).—Posterolateral margin with 8–16 setae, anterior margin of dorsal spine with scattered setules. Pereiopod buds well developed, extending to midlength of basis of maxilliped 2; distal tip of first pereiopod bud bifid.

Antennule (Fig. 3B).—Bearing terminal group of 3 aesthetascs, 1 or 2 simple setae, and 1 or 2 minute setules; subterminal group consisting of 2 or 3 simple setae; minute spinule present near base; small endopod bud present.

Antenna (Fig. 3C).—With long terminal seta of exopod extending beyond tip of protopod; endopod bud subequal in length to exopod; length of spinous process approximately half length of rostrum.

Mandible.—With minute palp bud present (not illustrated).

Maxillule (Fig. 3D).—With 1 large plumose and 1 slender sparsely plumose seta present below base of endopod; basial endite with 5 stout, 3–4 slender marginal setae and 7–8 submarginal setae; coxal endite with 5 stout marginal and 9–10 slender marginal and submarginal setae.

Maxilla (Fig. 3E).—Scaphognathite with 26–30 plumose setae; distal lobe of basial endite with 2 submarginal and 6 marginal setae, proximal lobe with 2 submarginal and 5–6 marginal setae; distal lobe of coxal endite with 3 submarginal and 1–2 marginal setae, proximal lobe with 4 marginal and 3–4 submarginal setae.

Maxilliped 1 (Fig. 3F).—Coxa with small epipod on anterior margin, posterior margin with 3 plumose setae; distal segment of endopod with 5 terminal and 1 subterminal setae, otherwise, setation pattern of endopod similar to zoea II; exopod bearing 13–14 natatory setae.

Maxilliped 2 (Fig. 3G).—Posterior mar-

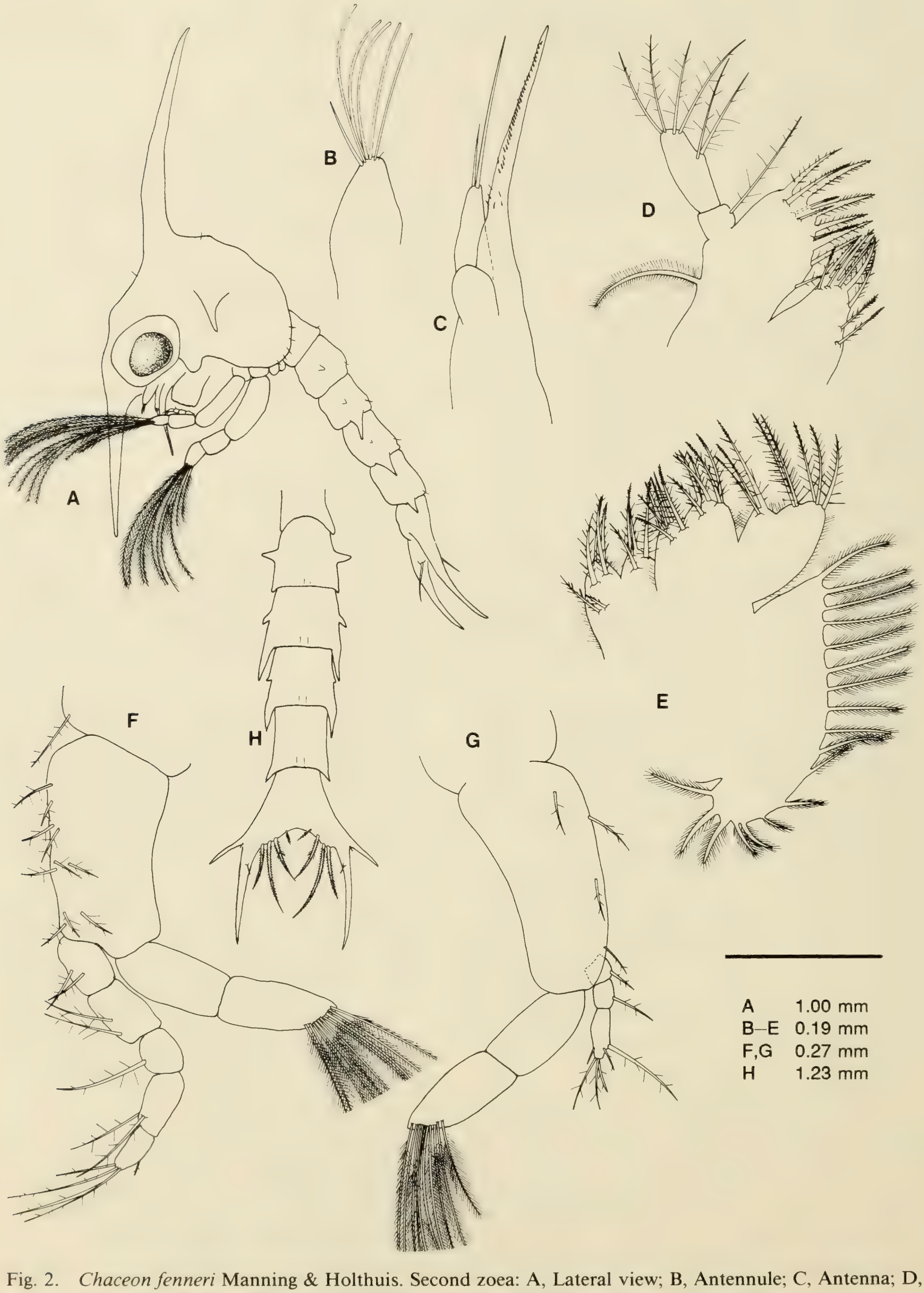


Fig. 2. *Chaceon fenneri* Manning & Holthuis. Second zoea: A, Lateral view; B, Antennule; C, Antenna; D, Maxillule; E, Maxilla; F., Maxilliped 1; G, Maxilliped 2; H, Abdomen and telson (dorsal view).

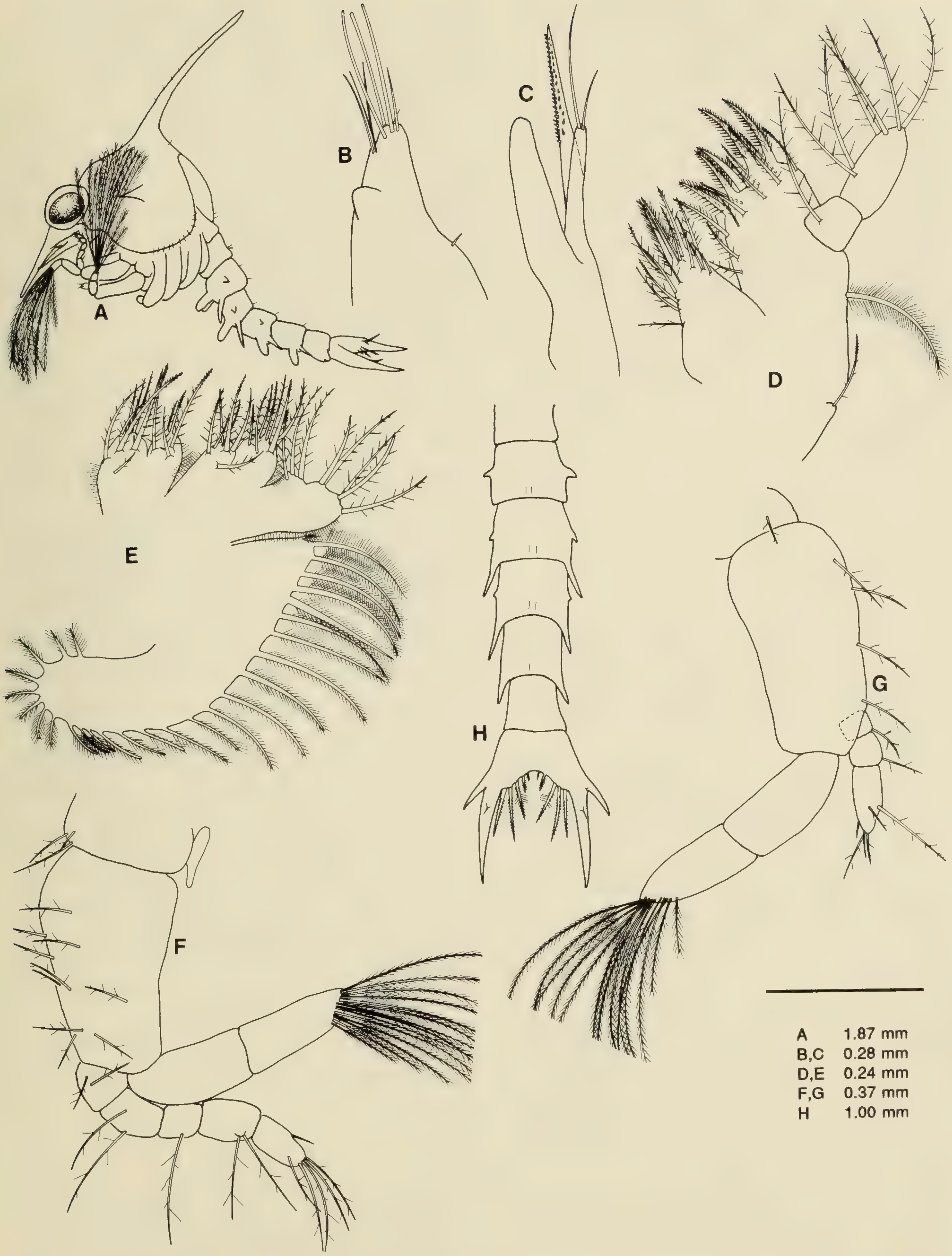


Fig. 3. *Chaceon fenneri* Manning & Holthuis. Third zoea: A, Lateral view; B, Antennule; C, Antenna; D, Maxillule; E, Maxilla; F, Maxilliped 1; G, Maxilliped 2; H, Abdomen and telson (dorsal view).

gin of coxa with 1 short plumose seta; pattern of setation on basis and endopod unchanged from zoea II; exopod bearing 14–15 natatory setae.

Maxilliped 3.—Present as minute bud (not illustrated).

Abdomen (Fig. 3A, H).—Six-segmented, first somite with 2–3 setae on dorsal surface, somites 2 and 3 similar to zoea II; presence of small dorsolateral spines on somite 4 variable, 48% of specimens examined bearing paired spines, 39% with spine present on only one side, 13% lacking dorsolateral spines; somite 5 as in zoea II; somite 6 lacking setae, dorsolateral spines, and lateral projections.

Telson (Fig. 3H).—Posterior margin bearing 2 pairs of small serrate spines between larger spines.

Zoea IV

Carapace (Fig. 4A).—With scattered setules above eye; posterolateral margin with 15–25 setae. Distal tip of first pereiopod bud chelate; other pereiopod buds showing segmentation.

Antennule (Fig. 4B).—With terminal group of 4 long aesthetascs and 2–3 simple setae of variable length, distal subterminal group consisting of 3 long and 5 short aesthetascs, proximal group consisting of 1–2 (rarely 3) simple setae; endopod bud well developed; basial lobe large, bearing 3–5 short setules.

Antenna (Fig. 4C).—With spinous process of protopod slightly less than half length of rostrum; endopod well developed, extending beyond distal tip of protopod, appearing incompletely segmented; exopod ¾ length of protopod, short terminal seta subequal in length to protopod.

Mandible (Fig. 4D).—With palp well developed, bearing 2–3 terminal sparsely plumose setae.

Maxillule (Fig. 4E).—With 1 large plumose and 1 or 2 slender sparsely plumose setae present proximal to base of endopod; basial endite with 7 stout, 4–5 (rarely 6) slender marginal and 9–10 (rarely 11) slender submarginal setae; coxal endite with 1–2 slender and 5 stout marginal setae, and 10–11 slender submarginal setae.

Maxilla (Fig. 4F).—Scaphognathite with 38–50 plumose setae; distal lobe of basial endite with 5–6 marginal and 5 submarginal setae, proximal lobe with 3–4 marginal and 4 submarginal setae; distal lobe of coxal endite with 2 marginal and 4–5 submarginal setae, proximal lobe with 6 marginal and 5–6 submarginal setae.

Maxilliped 1 (Fig. 4G).—Anterior margin of coxal segment with well developed epipod, posterior margin with 5–6 sparsely plumose setae; setation pattern of basis and endopod similar to zoea III; exopod bearing 17–18 (rarely 19) natatory setae.

Maxilliped 2 (Fig. 4H).—Setation pattern of coxal and basial segments and endopod similar to zoea III; exopod bearing 17–19 (rarely 20) natatory setae.

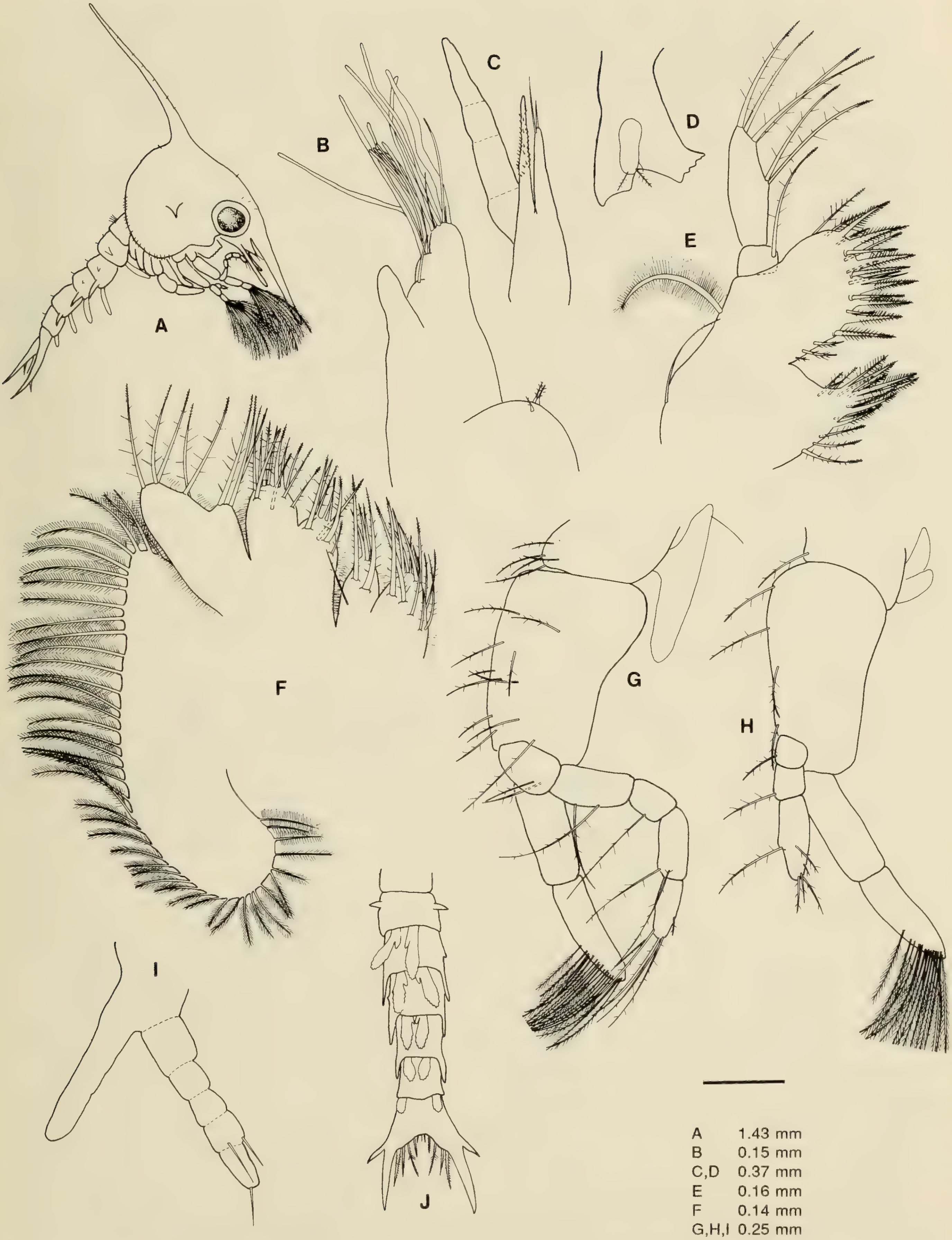
Maxilliped 3 (Fig. 4I).—Endopod 5-segmented, bearing 1–2 slender spines on distal segments; exopod well developed, unsegmented.

Abdomen (Fig. 4A).—With cluster of 3–5 setae on dorsal surface of first somite; presence of small dorsolateral spines on somite 4 variable, 50% of specimens examined bearing paired spines, 42% with single spine present on only one side, 8% lacking dorsolateral spines; abdominal somite 6 with few dorsal setae; pleopod buds much longer than in previous stage, buds on segments 2–4 with endopod developing.

Telson (Fig. 4J).—With 5 (rarely 4) small spines within central arch of posterior margin.

Megalopa

Carapace (Fig. 5A).—Rectangular in general outline, lacking dorsal and lateral spines, hepatic and branchial lobes present, setation sparse on dorsal surface, numerous setae present along posteroventral margins; rostrum well developed, strongly deflected ventrally between eye-stalks, tip bifid.



A	1.43 mm
B	0.15 mm
C,D	0.37 mm
E	0.16 mm
F	0.14 mm
G,H,I	0.25 mm
J	1.0 mm

Fig. 4. *Chaceon fenneri* Manning & Holthuis. Fourth zoea: A, Lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped 1; H, Maxilliped 2; I, Maxilliped 3; J, Abdomen and telson (dorsal view).

Antennule (Fig. 5B).—With basial segment bulbous, bearing 3–4 long setae and group of shorter simple setae; second segment subequal in length to third segment, bearing 4–5 simple setae along posterodistal margin; third segment bearing group of 6–7 simple setae along distal margin; inner ramus unsegmented, bearing 1 short subterminal and 5 long terminal simple setae on distal tip and 1 short simple seta present at midlength; outer ramus composed of 4 segments, first segment lacking setae or aesthetascs, second segment bearing 10 aesthetascs, third segment bearing 9 aesthetascs and 1 dorsal simple seta, fourth segment with 6 proximal aesthetascs on base, distal tip with 1 terminal and 1 subterminal long plumose seta.

Antenna (Fig. 5C).—Consisting of 3-segmented peduncle and 8-segmented flagellum, third peduncular segment bearing 1 long and 2 short simple setae along distal margin, fifth flagellar segment with 2 long and 2–3 shorter simple setae present along distal margin, eighth (terminal) segment with 5 terminal and 1 subterminal simple setae; pattern of setation for remainder of antennal segments as illustrated.

Mandible (Fig. 5D).—Cutting surface with distinct medial tooth; palp 2-segment, proximal segment bearing stout spine on outer margin; 1 long plumose seta present on inner margin in some specimens; distal segment bearing 17–21 stiff plumose setae.

Maxillule (Fig. 5E).—Endopod incompletely segmented, bearing 4 long plumose setae along inner margin and 2 stout serrate spines on distal tip; basial endite bearing 32–33 setae on distal margin, and proximal row of 5 simple setae; coxal endite with 29–30 setae, type and pattern of setation as illustrated.

Maxilla (Fig. 5F, G).—Scaphognathite bearing 79–84 plumose marginal setae and 6 small submarginal spines; endopod unsegmented, bearing 5–6 plumose setae near insertion of scaphognathite, number and pattern of setae on inner margin of endopod highly variable, ranging in number from 0–7; basial endite bearing 11–12 marginal and 5–6 submarginal setae on distal lobe, 6–7 marginal and 5–6 submarginal setae on proximal lobe; coxal endite with 5–6 marginal and 3–4 submarginal setae on distal lobe, 12 marginal and 9 submarginal setae on proximal lobe; types of setae on basial and coxal lobes as illustrated.

Maxilliped 1 (Fig. 6A, B).—Endopod unsegmented, bearing 3–4 long setae near base, 4–5 short spine-like setae along outer distal margin, and 3–4 setae of varying lengths on inner distal margin; exopod 2-segmented, proximal segment with 4–5 simple setae along distal margin, distal segment bearing 3 long simple terminal setae; basial endite with 35–36 marginal and 10 submarginal setae; coxal endite with 24–26 setae scattered over entire surface of the lobe; types of setae on basial and coxal endites as illustrated; epipod bearing 18–20 long simple setae, 1 plumose seta and a few short spine-like setae.

Maxilliped 2 (Fig. 6C).—Coxal segment with 2 short marginal plumose setae and 5–7 simple submarginal setae; epipod well developed, bearing 2 small plumose setae near base and 10–11 long simple setae on distal half; basis of endopod appearing incompletely segmented in some specimens, bearing 4–5 simple setae on inner margin and several plumose and simple setae on lateral margins, terminal segment with 10 strong cuspidate setae of various sizes and 2–3 plumodenticulate setae, pattern of setation on other segments as illustrated.

Maxilliped 3 (Fig. 6D, E).—Coxal segment with 18–23 sparsely plumose setae of various lengths; epipod with proximal group of 6–8 sparsely plumose setae and 26–35 long simple setae on distal two-thirds; endopod 5-segmented, inner margin of basis bearing 4 small denticles and 26–30 sparsely plumose setae, distal segment with 16 strong serrate setae increasing in length from proximal margin to distal tip, setation on remaining segments as illustrated; exopod

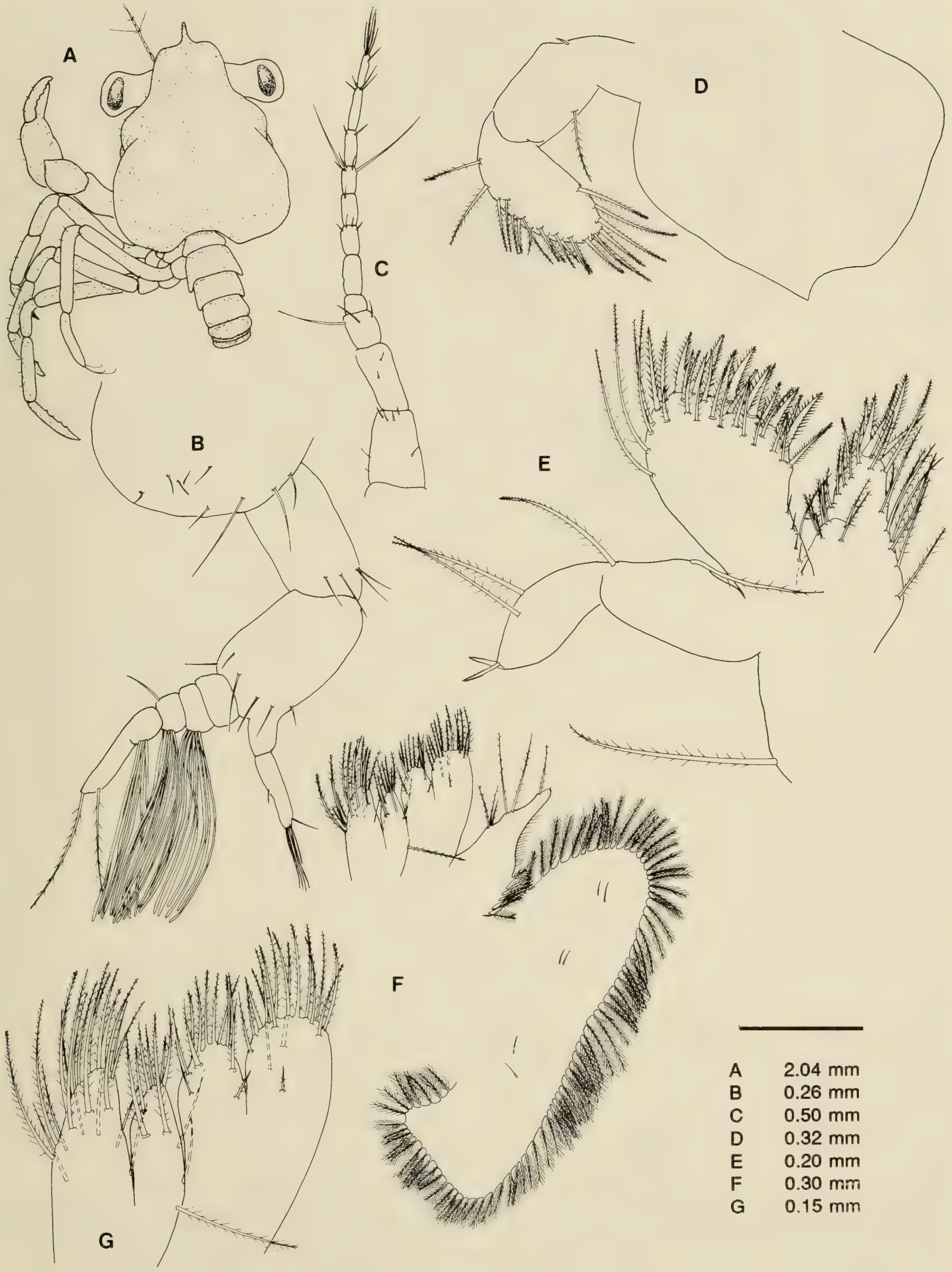


Fig. 5. *Chaecon fenneri* Manning & Holthuis. Megalopa: A, Dorsal view; B, Antennule; C, Antenna; D, Mandible and palp; E, Maxillule; F. Maxilla; G, Maxilla (coxal and basial endites).

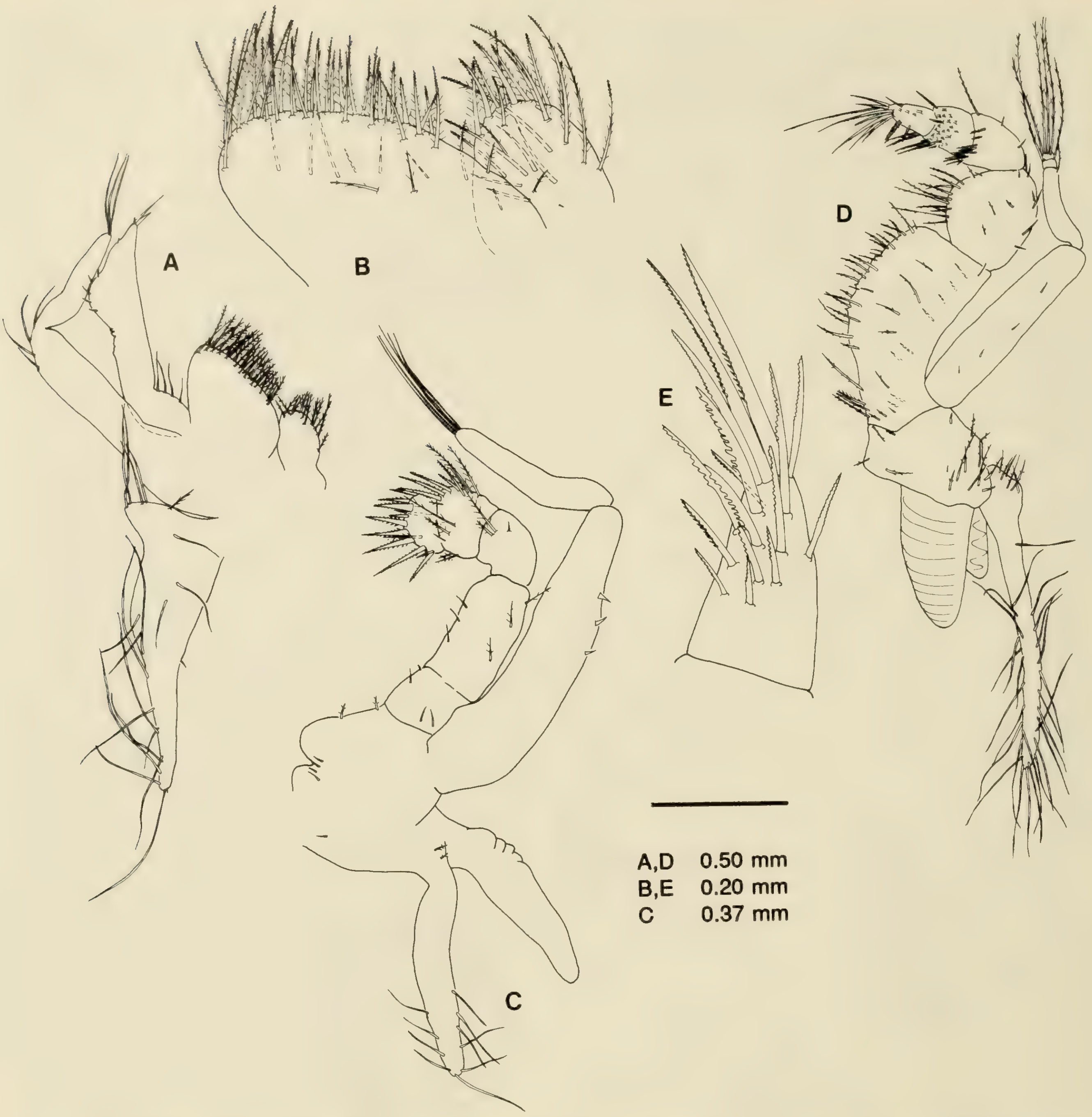


Fig. 6. *Chaceon fenneri* Manning & Holthuis. Megalopa: A, Maxilliped 1; B, Maxilliped 1 (coxal and basial endites); C, Maxilliped 2; D, Maxilliped 3; E, Maxilliped 3 (distal segment of endopod).

2-segmented, proximal segment bearing 4 short spines on lateral margin, tip of distal segment subdivided, bearing 1 short and 6 long plumose setae.

Pereiopod 1 (Fig. 7A).—Chelate, cutting edge of propodus bearing 5 teeth, ischium with strong hooked spine; pereiopods 2–4 (Fig. 7B–E) with spine on ventral side of coxa and row of 7–8 small spines on dactyl; propodus of pereiopod 5 with 3 strong spines, dactyl with 3 long hooked serrate setae.

Abdomen (Fig. 7G).—Composed of 6 segments and telson; segments 2–5 with blunt lateral processes.

Pleopods (Fig. 7H–J).—Present on abdominal segments 2–6; exopods of pleopods 1–4 bearing 29–31, 29–30, 27, and 23–24 plumose swimming setae, respectively; endopods of pleopods (Fig. 7I) 1–4 bearing 6,

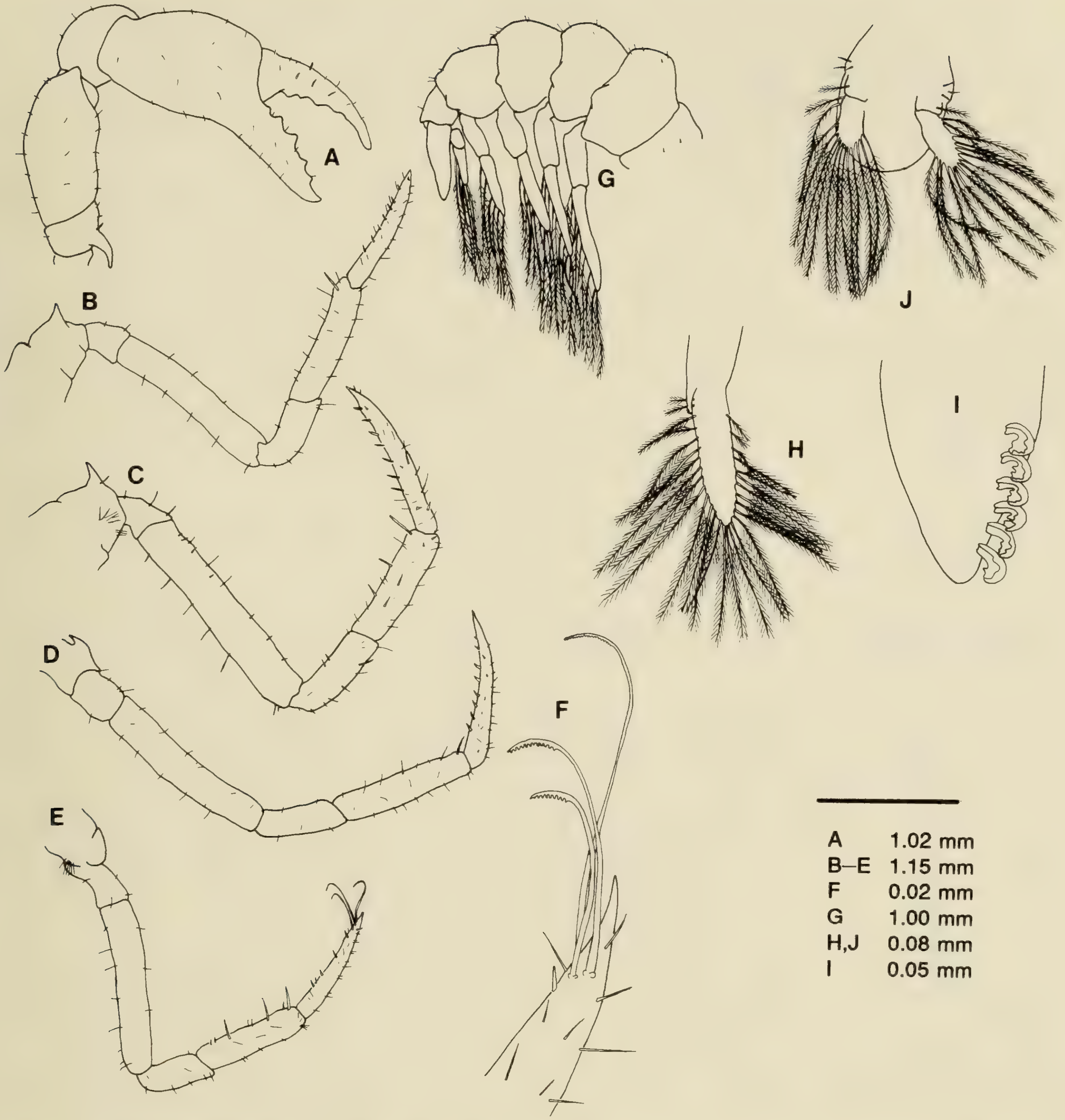


Fig. 7. *Chaceon fenneri* Manning & Holthuis. Megalopa: A, Chela (pereiopod 1); B, Pereiopod 2; C, Pereiopod 3; D, Pereiopod 4; E, Pereiopod 5; F, Dactyl of pereiopod 5; G, Lateral view of abdomen; H, Pleopod 2; I, Exopod of pleopod 2; J, Telson and pleopod 5.

6, 5, and 4–5 stout hooked spines, respectively; pleopod 5 (Fig. 7J) lacking endopod, bearing 1 plumose seta on basial segment and 14–15 plumose setae on exopod.

Discussion

Brattegard & Sankarankutty (1967) described a prezoea and first zoea of *Geryon tridens* hatched from a female collected south of Bergen, Norway. The complete larval development of *Chaceon quinquedens* under laboratory conditions was described by Perkins (1973) using larvae obtained from an ovigerous female collected off Delaware Bay. Ingle (1979) described the complete larval development of *G. tridens* reared in the lab-

Table 2.—Comparison of selected morphological characters in laboratory reared *Chaceon fenneri, C. quinquedens* as described by Perkins (1973), and *Geryon trispinosus* as described by Ingle (1979). Numbers in parentheses indicate mean or most frequent count. TSL = total spine length, TL = total length, CL = carapace length, DSL = dorsal spine length, SW = spine width, S = setae, Aes = aesthetascs, ND = no data, Sp = spines.

	Zoea I		
	C. fenneri	*C. quinquedens**	*G. tridens*
Morphometrics (in mm)			
TSL	2.50–(2.63)–2.90	2.65–(2.89)–3.06	2.6–2.8
CL	0.95–(1.02)–1.80	1.05–(1.14)–1.20	0.8–0.9
DSL	1.05–(1.08)–1.15	1.18–(1.30)–1.38	ND
SW	1.55–(1.66)–1.78	1.73–(1.93)–2.10	ND
Antennule setation	2 Aes + 2 S	4 Aes + 1 S	2 Aes + 2 S
Maxillule setation			
Basal endite	6 S	6 S	6 S
Coxal endite	(7)–8 S	6 S	9 S
Maxilla setation			
Basial endite	5 ± 4 S	5 + 5 S	6 + 5 S
Coxal endite	4 + 3 S	3 + 3 S	4 + 3 S
Scaphognathite	6–(7)–8 S	7 S	8 S
Maxilliped 2 setation			
Endopod terminal segment	5 + 1 S	4 + 1 S	4 + 1 S
	Zoea II		
	C. fenneri	*C. quinquedens**	*G. tridens*
Morphometrics (in mm)			
TSL	3.01–(3.41)–3.62	3.11–(3.29)–3.52	3.4–3.6
CL	1.10–(1.20)–1.37	1.10–(1.27)–1.40	1.2–1.3
DSL	1.20–(1.38)–1.62	1.20–(1.41)–1.53	ND
SW	1.80–(1.97)–2.18	1.95–(2.18)–2.35	ND
Antennule setation	5 Aes + 1–(2) S	4 Aes + 2 S	6 Aes
Maxillule setation			
Basial endite	11	12	11
Coxal endite	10	11	10–11
Maxilla setation			
Basial endite	6 + 5–(6) S	7 + 5 S	7 + 7 S
Coxal endite	4 + (5)–6	4 + 4 S	4 + 4 S
Scaphognathite	18 S	22 S	18 S
Maxilliped 1 setation			
Natatory	10	10–11	9–10
Maxilliped 2 setation			
Endopod terminal segment	5 + 1 S	4 + 1 S	5 + 1 S
Natatory	10–11	11	9–10
	Zoea III		
	C. fenneri	*C. quinquedens**	*G. tridens*
Morphometrics (in mm)			
TSL	4.03–(4.36)–4.59	4.03–(4.38)–4.67	4.0–4.2
CL	1.45–(1.58)–1.78	1.70–(1.75)–1.83	1.5–1.6
DSL	1.56–(1.77)–1.95	1.75–(1.81)–1.90	ND
SW	2.50–(2.64)–2.75	2.45–(2.68)–2.91	ND

Table 2.—Continued.

	Zoea III		
	C. fenneri	*C. quinquedens**	*G. tridens*
Antennule setation	3 Aes + 4–(5) S	7 Aes + 3 S	6 Aes + 2 S
Mandible palp	Present	Present	Present
Maxillule setation			
Basial endite	15–(16)–17 S	17 S	18 S
Coxal endite	14–(15) S	17 S	12–13 S
Maxilla setation			
Basial endite	8 + (7)–8 S	7 + 5 S	8 + 8 S
Coxal endite	(4)–5 + (7)–8 S	5 + 9 S	4 + 6 S
Scaphognathite	26–(28)–30 S	31 S	25–29 S
Maxilliped 1 setation			
Natatory	13–(14) S	14 S	12–14 S
Maxilliped 2 setation			
Endopod terminal segment	5 + 1 S	5 + 1 S	5 + 1 S
Natatory	(14)–15 S	12–14 S	12–14 S
	Zoea IV		
	C. fenneri	*C. quinquedens**	*G. tridens*
Morphometrics (in mm)			
TSL	5.00–(5.78)–6.32	5.00–(5.73)–6.12	4.9–5.2
CL	2.04–(2.34)–2.50	2.30–(2.44)–2.55	1.8–2.0
DSL	2.04–(2.31)–2.70	2.09–(2.32)–2.45	ND
SW	2.96–(3.29)–3.57	3.30–(3.56)–3.77	ND
Antennule setation	12 Aes + 3–6 S	12 Aes + 2 S	11 Aes + 3 S
Maxillule setation			
Basial endite	20–(21)–24 S	22 S	24 S
Coxal	16–(17)–18 S	17 S	17 S
Maxilla setation			
Basial endite	10–(11) + 7–(8) S	12 + 9 S	11 + 10 S
Coxal endite	(5)–6 + (11)–12 S	5 + 9 S	5 + 8 S
Scaphognathite	38–(44)–50 S	54 S	40–42 S
Maxilliped 1 setation			
Natatory	17–(18)–19 S	17 S	16–17 S
Maxilliped 2 setation			
Natatory	17–(18)–20 S	19 S	17–18 S
Telson inner arch (additional setae)	4–(5)	(4)–5	6
	Megalopa		
	C. fenneri	*C. quinquedens**	*G. tridens*
Morphometrics (in mm)			
CL	3.15–3.40	3.02–3.26	3.0–3.1
TL	5.30–5.90	6.32–6.60	ND
Maxillule setation			
Endopodite	2 Sp + 4 S	1 Sp + 3 S	6 S
Basial endite	37–(38) S	35 S	26–27 S
Coxal endite	29–30 S	25 S	17 S

Table 2.—Continued.

	Megalopa		
	C. fenneri	*C. quinquedens**	*G. tridens*
Maxilla setation			
Basial endite	16–(18) + 11–(12)–13 S	14 + 11 S	11 + 8 S
Coxal endite	8–(9)–10 + 21 S	8 + 16 S	6 + 13–14 S
Scaphognathite	79–(82)–84 S	approx. 100 S	62–63 S
Maxilliped 1 setation			
Exopod			
Terminal segment	3 S	5 S	3 S
Proximal segment	4–5 S	6 S	5 S
Basial endite	45–(46) S	37 S	33–34 S
Coxal endite	24–26 S	12 S	?
Epipod	18–(20)–21 S	16–18 S	10–12 S
Maxilliped 2 setation			
Exopodite			
Proximal segment	3 Sp	4 Sp	0 Sp
Distal segment	5 S	5 S	4 S
Endopodite	3 S	3 S	0 S
Carpus	12–13 S	13 S	7 Sp + 1 S
Maxilliped 3 setation			
Endopod terminal segment	16 S	12 S	9 S
Exopod terminal segment	7 S	6 S	5 S
Dactyl of last pereiopod (long hooked serrate setae)	3	2	3

* Measurements of TSL, CL, DSL, SW taken from specimens reared in the present study, other characters as described by Perkins (1973).

** All measurements and characters as described by Perkins (1973).

oratory from an ovigerous female taken in waters off Scotland. Larvae of those two species resemble the larvae of *C. fenneri* as described in the present study except for the specific differences listed in Table 2.

The zoeae of *C. fenneri,* particularly in the early stages, appear to be more similar to *G. tridens* than *C. quinquedens.* Larvae of *G. tridens* and *C. fenneri* both lack a dorsolateral spine on the fifth abdominal segment in all zoeal stages. Number of setae on the scaphognathite of these two species also tends to be more alike when compared to *C. quinquedens.* The larvae of *G. tridens* obviously differ from *C. fenneri* in lacking a mandibular palp in the third zoeal stage and having six additional short setae in the central arch of the telson posterior margin compared to four or five in *C. fenneri.*

The distribution of *C. fenneri* and it's congener, *C. quinquedens,* is sympatric in the western North Atlantic and Gulf of Mexico and larvae of both species may be simultaneously present in plankton samples (Perry et al. 1991). It would therefore be useful when studying the larval distribution of these commercially important species to be able to easily distinguish their larvae. Zoeae and megalopae of *C. fenneri* were compared to those of *C. quinquedens* as described by Perkins (1973) as well as zoeae I–IV of *C. quinquedens* reared from the Gulf of Mexico during the present study. There are several morphological differences that allow the zoeae of these two species to be separated (Table 2). The single most useful character is the presence of a dorsolateral spine (usually but not always paired) on the

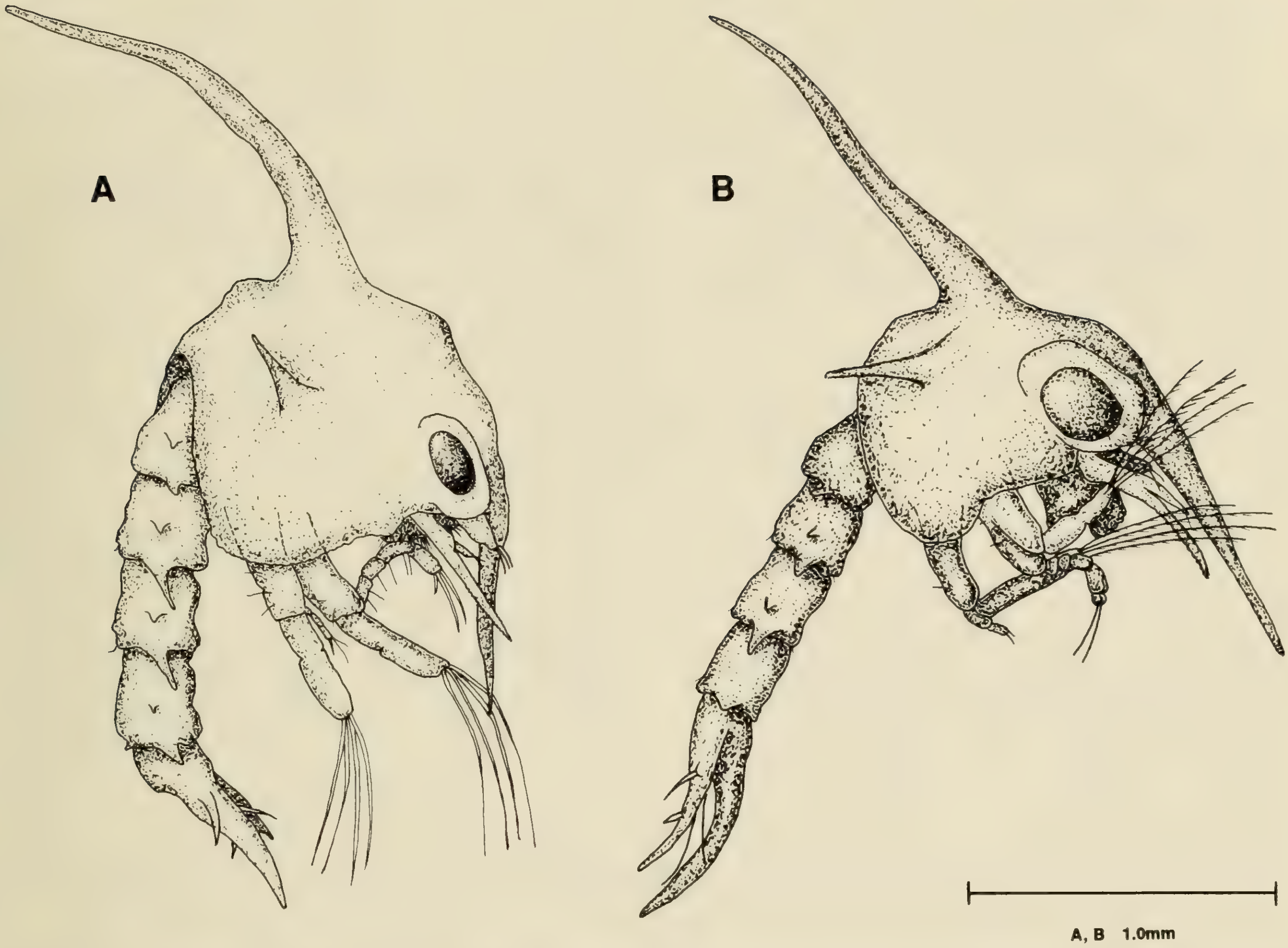


Fig. 8. Comparison of first zoea of *Chaeceon fenneri* Manning & Holthuis (A), and *Chaceon quinquedens* Smith (B) hatched from females collected from the Gulf of Mexico.

fifth abdominal segment of all zoeal stages of *C. quinquedens.* This spine is never present on zoeae of *C. fenneri.* The first zoea of *C. fenneri* is smaller than the first zoea of *C. quinquedens.* The dorsal spine of zoea I in *C. quinquedens* appears much more recurved (Fig. 8) when compared to zoea I of *C. fenneri*; however, this difference, as well as the difference in size of larvae, is less obvious in later zoeal stages. Telson shape can also be used to distinguish the zoeae of *C. fenneri* and *C. quinquedens* (Fig. 9). The proximal portion of the telson appears more constricted in *C. fenneri* compared to the corresponding stage in *C. quinquedens.* The telson of zoea IV of *C. quinquedens* bears 4 (rarely 5) short setae in addition to the 3 pairs of long inner arch setae, compared to 5 (rarely 4) short setae in *C. fenneri.*

Megalopae of *C. fenneri* and *C. quinquedens* can be separated based on the number of long, hooked, serrate setae on the dactyl of the last pereiopod (3 in *C. fenneri*, 2 in *C. quinquedens*). In this study we were unable to rear *C. quinquedens* beyond zoea IV, therefore, the utility of this character to separate megalopae of these species has not been confirmed with specimens from the Gulf of Mexico.

The large size and general appearance of *Chaceon* larvae can be used to separate them from almost all other non-geryonid brachyuran larvae found in the Gulf of Mexico. Three exceptions to this are the zoeae of *Ovalipes floridanus* Hay & Shore, *Menippe mercenaria* Say, and *M. adina* Williams & Felder. Although the adult distribution of all three species is restricted to coastal waters, the distribution of their larvae extends out into relatively deep shelf waters (Trues-

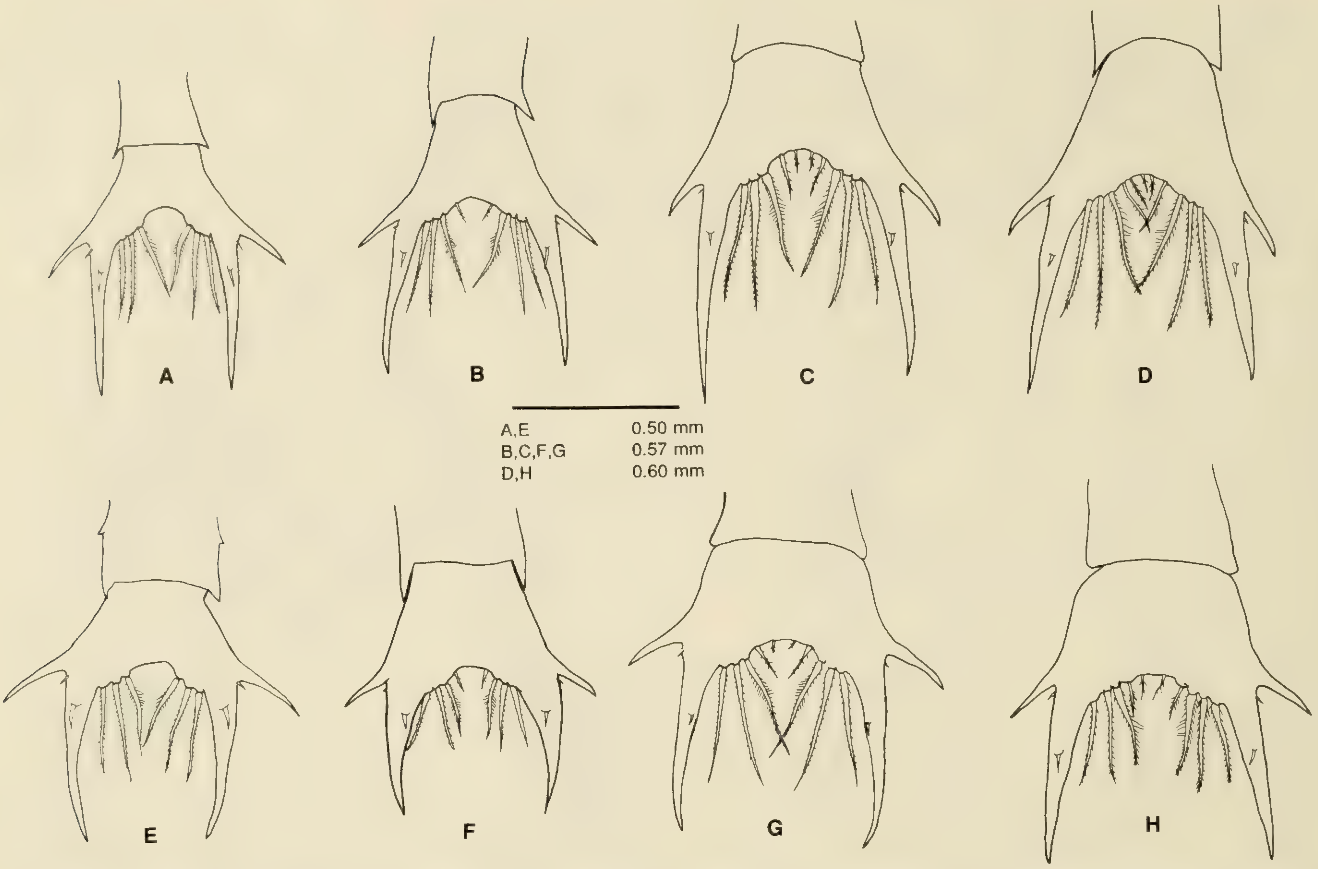


Fig. 9. Telsons of zoeae I–IV of *Chaceon quinquedens* Smith (A–D), and *Chaceon fenneri* Manning & Holthuis (E–H) hatched from females collected from the Gulf of Mexico.

dale & Andryszak 1983; Stuck, personal observation) where larvae of *Chaceon* occur (Perry et al. 1991). Zoeae of *M. mercenaria* have dorsolateral spines on abdominal segments 4 and 5, similar to the zoeae of *Chaceon quinquedens* except that the dorsolateral spines on the fifth segment are much larger than those on the fourth (Porter 1960). In *C. quinquedens* the dorsolateral spine on the fifth segment is slightly smaller than that of the fourth. The zoeae of *M. adina* (Stuck, personal observation) also have a large dorsolateral spine on the fifth abdominal segment, but completely lack this spine on the fourth segment, allowing *M. adina* to be separated from both *C. fenneri* and *C. quinquedens.* Zoeae of both species of *Menippe* lack large lateral spines on the telson which are present in all geryonid zoeae. Megalopae of *Menippe adina* were described by Martin et al. (1988), and may be separated from the megalopae of *Chaceon* by their large robust chela, and smaller overall size.

Larvae of *O. floridanus* have been found in plankton samples from the northern Gulf of Mexico during winter months (Stuck, personal observation). Early stage zoeae (I–III) of *O. floridanus* and *O. ocellatus* (Herbst) (Costlow & Bookhout 1966) have dorsolateral spines on the fourth and fifth abdominal segments but lose the spines on the fourth segment in later zoeal stages. The zoeae of *Ovalipes* are smaller, with a different overall shape, and the telson has much smaller lateral spines than the zoeae of species of *Chaceon.* The megalopae of *Ovalipes* are much smaller than the megalopae of *Chaceon.* The megalopae of *O. floridanus* have a large dorsal keel extending from the carapace that is not found in *Chaceon.* Additional characters useful in distinguishing geryonid larvae from morphologically similar non-geryonid larvae, and possible phylogenetic relationships, are discussed by Ingle (1979) and Rice (1980).

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NEW SPECIES OF FRESH-WATER CRABS OF THE GENUS *NEOSTRENGERIA* (CRUSTACEA: DECAPODA: PSEUDOTHELPHUSIDAE) FROM COLOMBIA

Martha R. Campos

Abstract.—Six new species and one new subspecies of the genus *Neostrengeria* Pretzmann, 1965, are described: *N. aspera, N. gilberti, N. lobulata, N. macarenae, N. tencalanensis, N. tonensis* and *N. libradensis appressa.* With the addition of the new species, the endemic genus *Neostrengeria* now comprises 18 species distributed on the western and the eastern slopes of the Eastern Cordillera of the Andes of Colombia, at altitudes ranging from 400 to 3000 m above sea level.

The genus *Neostrengeria* Pretzmann, 1965, comprises a group of small pseudothelphusid crabs inhabiting mountain streams in the Eastern Cordillera of Colombia. The systematics of the genus were established by Rodríguez (1982) and its geographical distribution has been discussed by Campos & Rodríguez (1985). Examination of material collected during a recent survey along the Eastern Cordillera revealed the presence of six new species and one new subspecies within the previously known distribution of the genus. This material is deposited at the Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb. and cl. are used for carapace breadth and carapace length, respectively.

Family Pseudothelphusidae
Rathbun, 1893
Tribe Hypolobocerini Pretzmann, 1971
Genus *Neostrengeria* Pretzmann, 1965
Neostrengeria aspera, new species
Fig. 1

Material examined.—Los Pozos, Vereda Hinche Alto, Municipio La Palma, Cundinamarca Department, 1600 m alt., 22 Oct 1990, G. Acosta: 1 male holotype, cb. 25.5 mm, cl. 14.8 mm; 3 male paratypes, cb. 25.1, 23.4, 22.6 mm, cl. 14.5, 14.0, 13.9 mm; 2 female paratypes, cb. 23.5, 20.5 mm, cl. 14.1, 12.6 mm (ICN-MHN-CR 1192). Quebrada La Olla del Relleno, Vereda Hinche Alto, Municipio La Palma, Cundinamarca Department, 1600 m alt., 22 Oct 1990, G. Acosta: 4 male paratypes, cb. 25.4, 18.7, 18.2, 17.9 mm, cl. 14.6, 11.6, 11.3, 11.0 mm; 2 female paratypes, cb. 19.3., 17.7 mm, cl. 12.1, 10.6 mm (ICN-MHN-CR 1193).

Diagnosis.—Male gonopod with the accessory lobe elongated, flat caudally, irregular in shape, densely covered with spinulae on distal half giving lobe rough appearance.

Description.—Carapace with cervical groove straight and shallow, deeper in posterior half, ending far from lateral margin. Anterolateral margin with shallow depression behind orbit, followed by approximately 15 teeth regularly spaced on anterolateral half; posterior half smooth. Postfrontal lobes small and rounded, separated by two shallow depressions. Median groove shallow and narrow. Front with upper border ill defined in frontal view, bilobed with slight middle depression in dorsal view; lower margin strongly sinuous in frontal view. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions well defined.

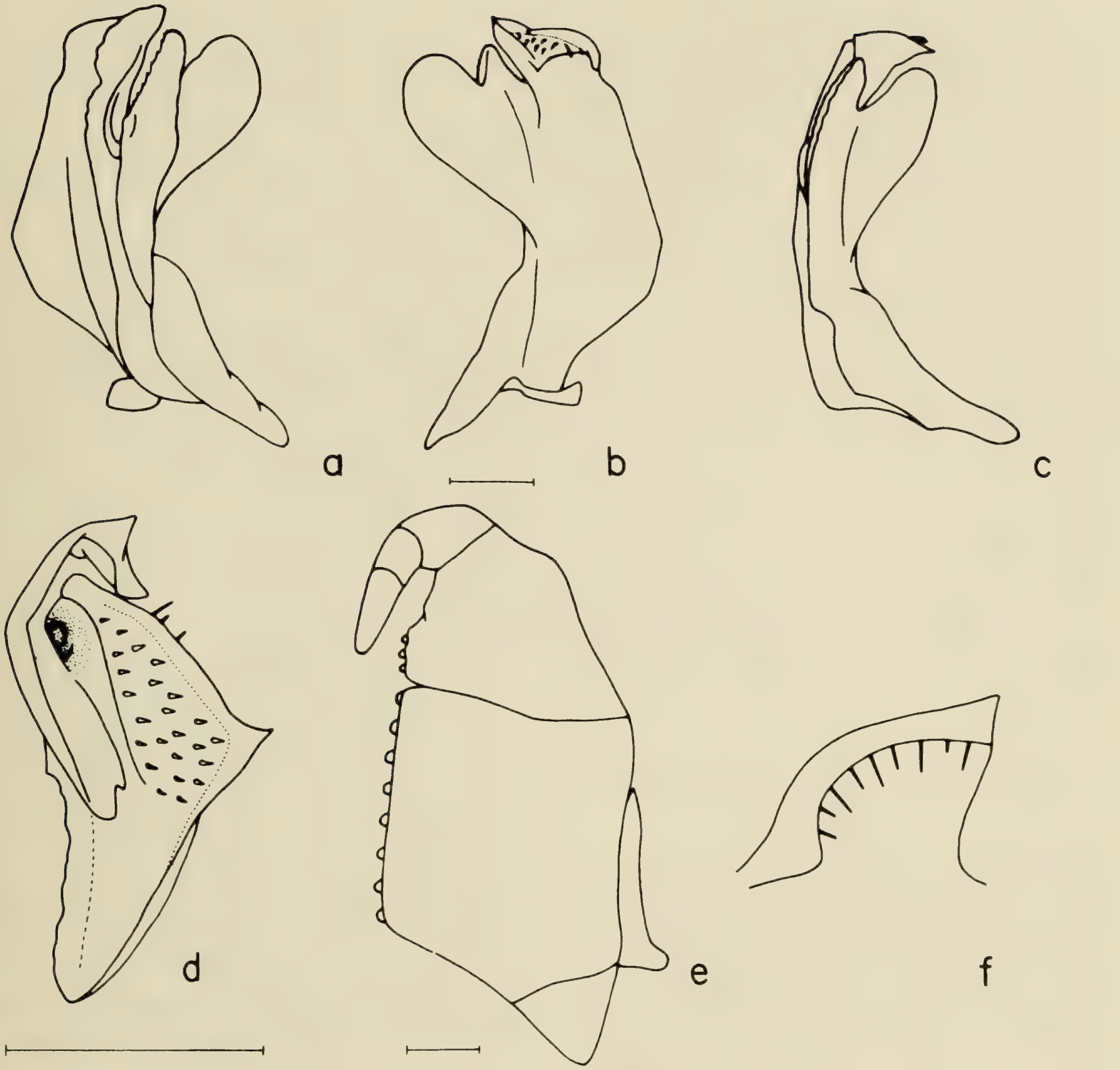

Fig. 1. *Neostrengeria aspera,* new species, holotype, ICN-MHN-CR 1192: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

Palm of larger chela strongly inflated, fingers gaping; palm of smaller chela moderately inflated, fingers not gaping. Distal half of palm and fingers each with small, dark papillae loosely arranged in rows. Walking legs each with five rows of large spines on dactylus, spines diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anterolateral and anteroventral rows with 4 spines, external row with 4 spines plus 1 papilla and 1 pair of proximal papillae, posteroventral and posterolateral rows with 3 spines. Merus of third maxilliped with acute angle on distal half of external margin; exognath of third maxilliped 0.72 length of ischium (Fig. 1e). Orifice of efferent branchial channel open (Fig. 1f).

Male gonopod moderately wide in caudal view, with mesial border slightly concave. Distolateral border with sinuous ridge, apical margin festooned. Accessory lobe elongated, as long as lateral lobe, flat caudally, irregular in shape, densely covered with spinules on distal half giving lobe rough appearance (Fig. 1a). Lateral lobe foliose, rounded in distal portion, separated from accessory lobe by deep notch (Fig. 1b, c). Apical portion formed by narrow expansion, with lateral border at right angle with cephalic and mesial borders; this angle continued by sharp spines in apical view. Mesial lobe small and triangular. Projection of spermatic channel awl-shaped, with small ridge on inner side (Fig. 1d).

Etymology.—The specific name is from the Latin "asper" for rough, in reference to the roughened aspect of the accessory lobe of the gonopod.

Remarks.—This species resembles *Neostrengeria lindigiana* (Rathbun, 1897) in the shape of the male gonopod, but in *N. lindigiana* the apex is wider and formed by an oval expansion of the cephalic margin; the accessory lobe is spatulate, smaller and smooth.

Neostrengeria gilberti, new species
Fig. 2

Material examined.—Vereda Tierra Vieja, La Vega-Sasaima highway, Municipio La Vega, Cundinamarca Department, 1250 m alt., 20 Apr 1987, M. R. Campos: 1 male holotype, cb. 23.8 mm, cl. 14.6 mm; 6 male paratypes, cb. 24.7, 23.2, 23.0, 22.6, 22.1, 20.7 mm, cl. 15.0, 14.1, 14.0, 13.7, 13.4, 12.6 mm; 2 female paratypes, cb. 24.2, 20.6 mm, cl. 13.2, 12.2 mm (ICN-MHN-CR 0715).

Diagnosis.—Male gonopod with the lateral lobe very wide, foliose, rounded distally, separated from accessory lobe by deep notch. Basal setae implanted on prominent rounded lobe, set off from outline of margin.

Description.—Carapace with cervical groove straight and deep, ending near lateral margin. Anterolateral margin with shallow depression behind orbit, followed by series of papillae on anterolateral half; posterior half smooth. Postfrontal lobes small and rounded, limited anteriorly by two small depressions; carapace moderately inclined anteriorly in this region. Median groove absent. Front with upper border absent in frontal view, bilobed in dorsal view; lower margin strongly sinuous in frontal view. Lower orbital margin smooth. Surface of carapace smooth, covered by small papillae; regions not well delimited.

Palm of larger chela strongly inflated, fingers gaping; palm of smaller chela moderately inflated, fingers not gaping. Distal half of palm and fingers each with small, dark papillae loosely arranged in rows. Walking legs each with 5 rows of spines on dactylus; spines conspicuous, diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anterolateral and anteroventral rows with 4 spines, external row with 4 spines plus 1 pair of proximal papillae, posteroventral row with 2 spines and posterolateral row with 3 spines. Merus of third maxilliped with acute angle on distal half of external margin; exognath of third maxilliped 0.58 length of ischium (Fig. 2e). Orifice of efferent branchial channel open (Fig. 2f).

Male gonopod moderately wide in caudal view, with mesial border straight. Distolateral border with strong ridge. Accessory lobe elongated, forming narrow flat ridge in caudal view, as long as lateral lobe (Fig. 2a). Lateral lobe very wide, foliose, rounded distally, separated from accessory lobe by deep notch (Fig. 2b, c). Apical portion formed by oval expansion directed laterally, with conspicuous cephalic spine. Mesial lobe small. Projection of spermatic channel awl-shaped, with spinule on inner side (Fig. 2d). Basal setae implanted on prominent rounded lobe, set off from outline of margin (Fig. 2a).

Etymology.—This species is named in honor of the Venezuelan carcinologist Dr. Gilberto Rodríguez.

Remarks.—This species resembles *Neostrengeria lindigiana* (Rathbun, 1897) in the shape of the gonopod, but in *N. lindigiana* the accessory lobe is smaller and the lateral lobe narrower and kidney-shaped.

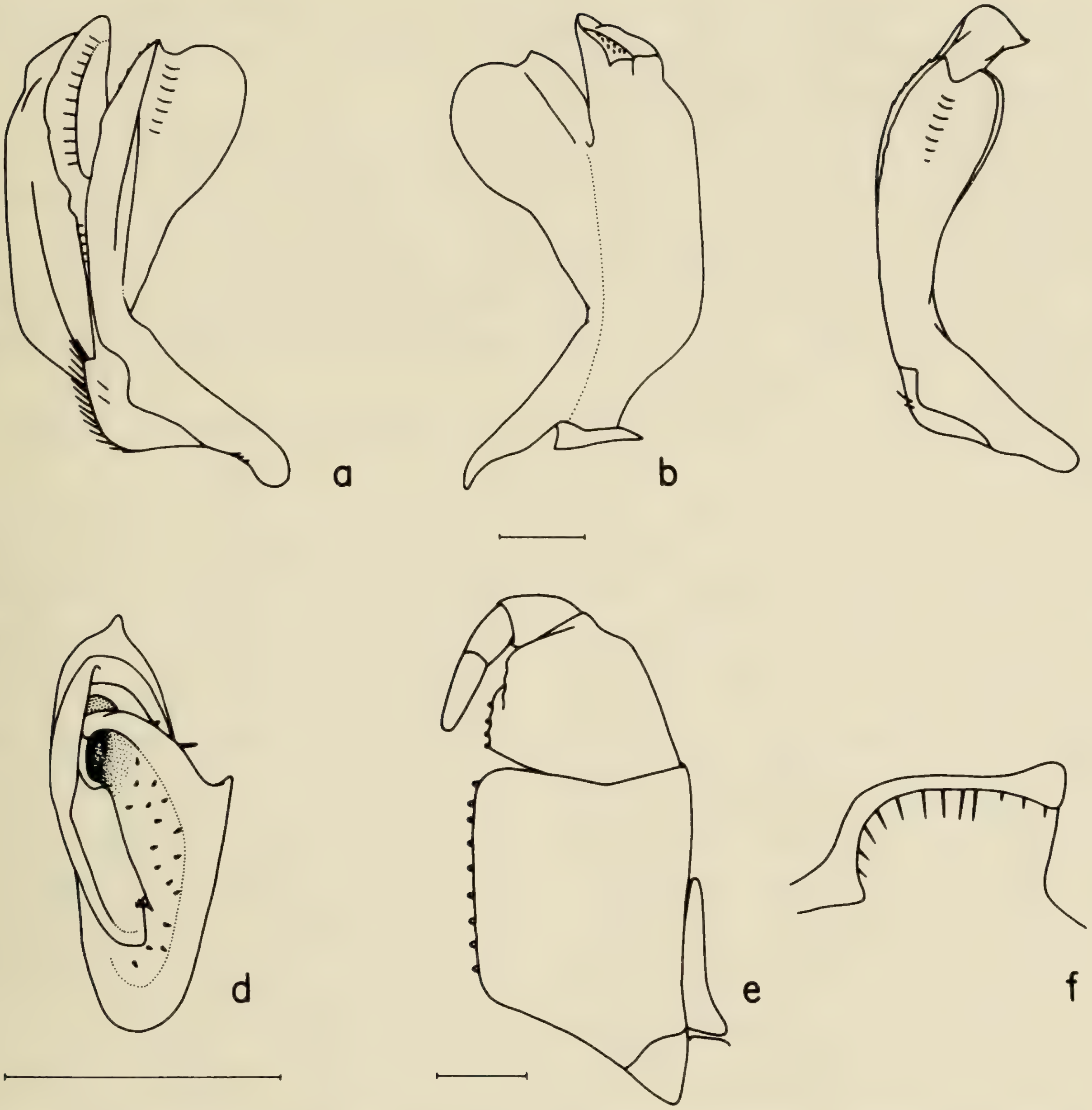

Fig. 2 *Neostrengeria gilberti,* new species, holotype, ICN-MHN-CR 0715: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

Neostrengeria libradensis appressa, new subspecies
Fig. 3

Material examined.—Puente Cojito, Vereda Manzanares, Chinácota-Ragonvalia highway, Municipio Chinácota, Norte de Santander Department, 1400 m alt., 28 Mar 1987, M. R. Campos: 1 male holotype, cb. 30.1 mm, cl. 17.2 mm; 7 male paratypes, cb. 29.4, 28.7, 28.4, 27.1, 24.7, 24.1, 22.5 mm, cl. 17.0, 16.9, 16.8, 16.3, 14.7, 14.6, 13.7 mm; 6 female paratypes, cb. 33.8, 27.8, 26.4, 25.9, 23.8, 21.5 mm, cl. 19.7, 16.6, 16.1, 15.6, 13.8, 12.9 mm (ICN-MHN-CR 0701).

Diagnosis.—Male gonopod with mesial border concave, with strongly subapical notch. Accessory lobe elongated and narrow on distal portion in caudal view, its distal margin continuous with distal margin of lateral lobe in lateral view. Accessory and lateral lobes attached to gonopod throughout their entire length.

Description.—Carapace with cervical groove straight and shallow, ending near lateral margin. Anterolateral margin with deep depression behind orbit, followed by 4 papillae on anterolateral half; posterior with 12 teeth. Postfrontal lobes wide, rounded, limited anteriorly by 2 small depressions. Median groove shallow. Front with upper border ill defined in frontal view, convex in dorsal view; lower margin strongly sinuous in frontal view. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions well defined.

Palm of larger chela strongly inflated, fingers not gaping; palm of smaller chela moderately inflated, fingers not gaping. Distal half of palm and fingers each with small, dark papillae loosely arranged in rows. Walking legs each with 5 rows of spines on dactylus; spines conspicuous, diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anterolateral and anteroventral rows with 6 spines plus 2 proximal papillae, external row with 5 spines plus 3 papillae and 1 pair of proximal papillae, posteroventral and posterolateral rows with 5 spines. Merus of third maxilliped with sharp angle on distal half of external margin; exognath of third maxilliped 0.62 length of ischium (Fig. 3e). Orifice of efferent branchial channel open (Fig. 3f).

Male gonopod moderately narrow in caudal view, mesial border concave, with strongly subapical notch. Distolateral border with straight ridge. Accessory lobe elongated and narrow on distal portion in caudal view, its distal margin continuous with distal margin of lateral lobe in lateral view. Lateral lobe elliptic. Accessory and lateral lobes attached to gonopod throughout their entire length (Fig. 3a, b, c). Apical portion oblong, with acute cephalic spine. Mesial lobe small and triangular. Projection of spermatic channel bifid (Fig. 3d).

Etymology.—The specific name is from Latin "adprimere," to lie flat against, and refers to the position of the accessory and lateral lobes in relation to the shaft of the gonopod.

Remarks.—This species resembles *Neostrengeria libradensis libradensis* Rodríguez, 1980 in the shape of the gonopod, but in *N. libradensis libradensis* the accessory lobe is spatulated in caudal view, its distal portion directed cephalically. Accessory lobe separated from lateral lobe by deep notch.

Neostrengeria lobulata, new species
Fig. 4

Material examined.—Quebrada Limoncito, Vereda Cuesta Rica, Municipio Cucutilla, Norte de Santander Department, 1700 m alt., 8 Oct 1988, M. R. Campos: 1 male holotype, cb. 22.4 mm, cl. 14.1 mm; 3 male paratypes, cb. 22.1, 22.0, 19.2 mm, cl. 13.5, 13.3, 12.4 mm; 3 female paratypes, cb. 24.6, 23.0, 20.2 mm, cl. 15.5, 14.7, 13.2 mm (ICN-MHN-CR 0925). Quebrada Guayabito, Vereda Guayabito, Municipio Cucutilla, Norte de Santander Department, 2150 m alt., 8 Oct 1988, M. R. Campos: 2 males, cb. 22.6, 19.5 mm, cl. 13.8, 12.6 mm; 2 females, cb. 21.6, 20.5 mm, cl. 13.5, 12.5 mm (ICN-MHN-CR 0923). Vereda San Miguel, Minicipio Cucutilla, Norte de Santander Department, 1700 m alt., 8 Oct 1988, M. R. Campos: 1 male, cb. 18.3 mm, cl. 12.4 mm; 1 female, cb 24.4 mm, cl. 16.7 mm (ICN-MHN-CR 0924).

Diagnosis.—Male gonopod narrow and constricted near middle. Distolateral margin widening distally to form bulbous projection covered by patch of strong, short, brown spines, which are continued over distal apical expansion.

Description.—Carapace with cervical groove straight and shallow, deep on posterior half, ending far from lateral margin. Anterolateral margin with a deep depression behind orbit, followed by series of papillae on anterolateral half; posterior half smooth. Postfrontal lobes rounded, high and indicated anteriorly by 2 depressions. Me-

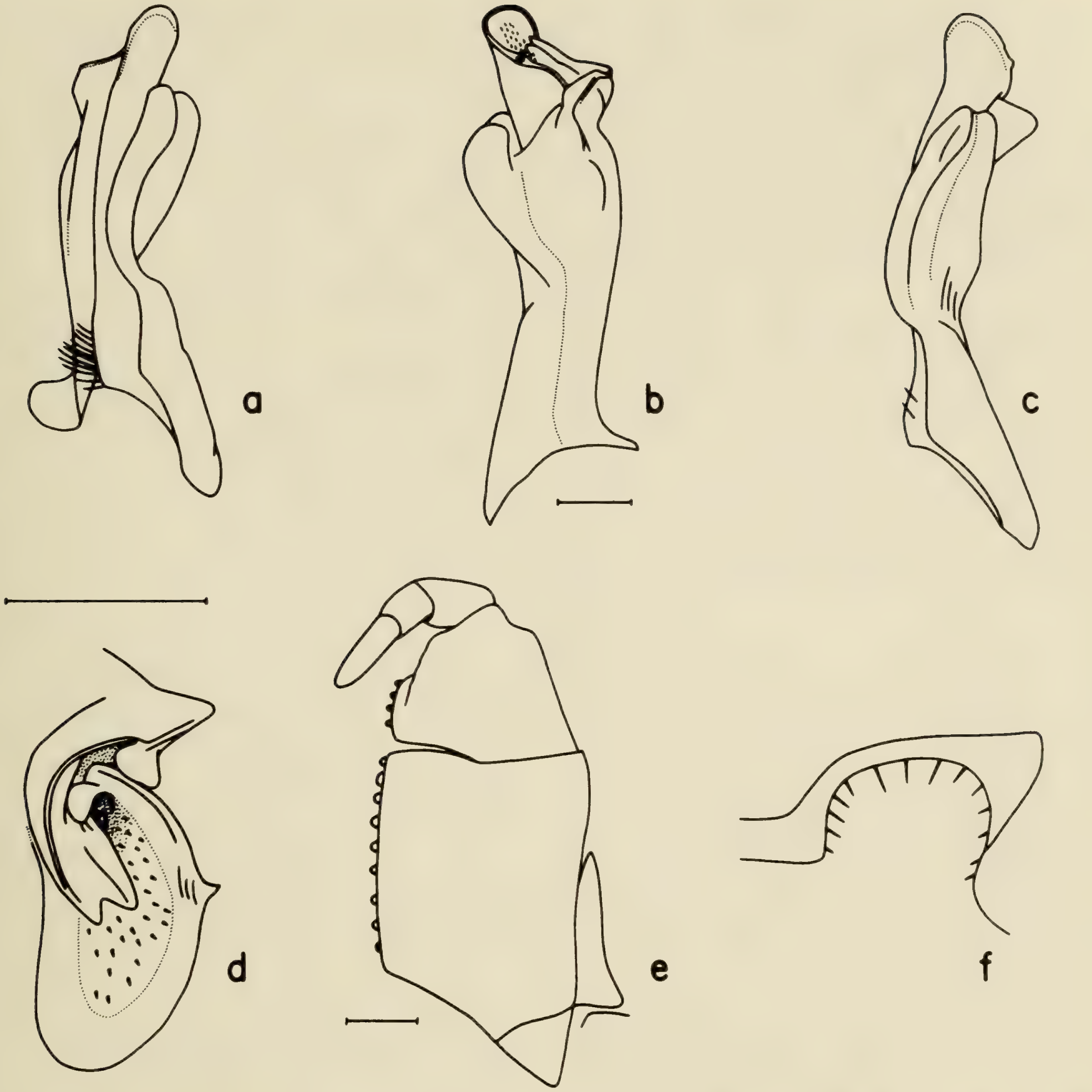

Fig. 3. *Neostrengeria libradensis appressa,* new subspecies, holotype, ICN-MHN-CR 0701: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

dian groove shallow. Surface of carapace behind orbit inclined anteriorly, but only slightly depressed towards midline. Front with upper border absent in frontal view, slightly bilobed in dorsal view; lower margin strongly sinuous in frontal view. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions strongly demarcated.

Palm of the larger chela strongly inflated, fingers gaping. Distal half of palm and fingers with small, dark papillae loosely arranged in rows. Walking legs each with 5 rows of spines on dactylus; spines conspicuous, diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anteroventral row with 5 spines plus 1 proximal papilla, anterolateral row with 5 spines, external row with 5 spines plus 1 papilla and 1 pair of proximal papillae, posteroventral and posterolateral rows with 5 spines. Merus of third maxilliped with a shallow depression on distal half of external margin; exognath of

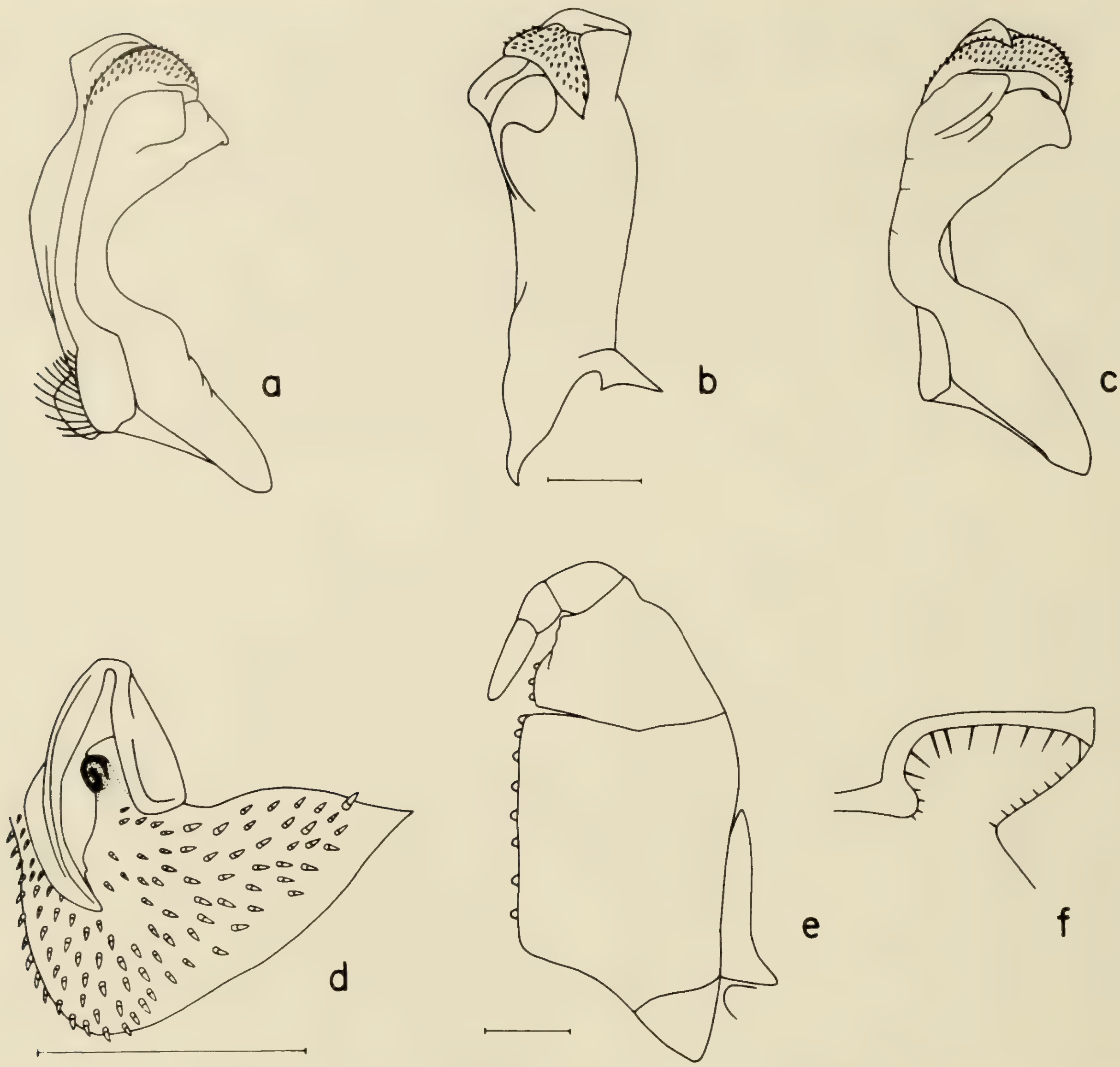

Fig. 4. *Neostrengeria lobulata,* new species, holotype, ICN-MHN-CR 0925: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

third maxilliped 0.65 length of ischium (Fig. 4e). Orifice of efferent branchial channel open (Fig. 4f).

Male gonopod narrow and constricted near middle in caudal view; mesial border strongly arched on subdistal portion with wide, deep notch. Accessory lobe long, narrow on proximal ¾ but wide on distal portion, as long as lateral lobe, and directed laterally. Lateral lobe elongated with irregular external margin, rounded on distal portion, strongly curved, directed cephalically. Distolateral margin widening distally to form bulbous projection covered by patch of strong, short, brown spines, which are continued over distal apical expansion (Fig. 4a, b, c). Apical portion formed by wide expansion, of irregular shape, with borders turned over and projected in an acute lobe. Mesial lobe rudimentary, represented by subterminal swelling. Projection of spermatic channel bifid, with narrow and acute points (Fig. 4d).

Etymology.—The specific name is from the Latin "lobulus" for lobe, in reference to the aspect of the apical expansion of the gonopod.

Neostrengeria macarenae, new species
Fig. 5

Material examined.—Caño Guayapa, Municipio El Piñal, Serranía de la Macarena, Meta Department, 400 m alt. 23 Feb 1962, H. Arévalo: 1 male holotype, cb. 42.5 mm, cl. 24.5 mm (ICN-MHN-CR 0758).

Diagnosis.—Male gonopod strongly wide in caudal view, with wide mesial border, forming rounded and conspicuous proximal lobe. Lateral lobe foliose espatulated expansion. Mesial lobe with wide basis, rounded distally, displaced proximally, with basal surface rough.

Description.—Carapace with cervical groove straight and shallow, not reaching margin of carapace. Anterolateral margin with deep depression behind orbit, followed by series of ill defined papillae. Postfrontal lobes wide, high. Median groove shallow. Surface of carapace behind front inclined anteriorly, but only slightly depressed towards midline. Front with upper border straight in dorsal view; well marked with row of conspicuous tubercles; lower margin strongly sinuous in frontal view. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions well delimited.

Larger chela elongated, with palm moderately inflated; fingers long and slender, with small dark papillae loosely arranged in rows. Walking legs each with 5 rows of spines on dactylus; spines small diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anteroventral and antrolateral rows with 5 spines plus 3 intercalated papillae, external row with 4 spines plus 2 intercalated papillae and 2 pairs of proximal papillae, posteroventral row with 4 spines and posterolateral row with 5 spines. Merus of third maxilliped with sharp angle on distal half of the external margin; exognath of third maxilliped 0.54 length of the ischium (Fig. 5e). Orifice of efferent branchial channel open (Fig. 5f).

Male gonopod strongly wide in caudal view with mesial border forming rounded and conspicuous proximal lobe. Gonopod gradually decreasing in width distally. Distolateral border slightly concave, with slender ridge. Accessory lobe narrow, oblong, and shorter than lateral lobe. Lateral lobe foliose espatulated expansion, with distal portion directed laterally (Fig. 5a, b, c). Apical portion narrow, with cephalic sharp spinule. Mesial lobe with wide basis, rounded distally, displaced proximally, with basal surface rough. Projection of spermatic channel awl-shaped, with a basal spinule on inner side (Fig. 5d).

Etymology.—The specific name refers to the Serranía de la Macarena, where the type was collected.

Remarks.—This species resembles *Neostrengeria macropa* (H. Milne Edwards, 1853) in the shape of the male gonopod, but in *N. macropa* the lateral lobe is narrower and elongated and the mesial lobe triangle-shaped.

Neostrengeria tencalanensis, new species

Fig. 6

Material examined.—Vereda Tencalá, Municipio Pamplona, Norte de Santander Department, 1700 m alt., 6 Oct 1988, M. R. Campos: 1 male holotype, cb. 23.3 mm, cl. 14.5 mm; 1 male paratype, cb. 21.7 mm, cl. 13.5 mm; 2 female paratypes, cb. 21.2, 19.5 mm, cl. 13.9, 10.7 mm (ICN-MHN-CR 0919). Quebrada Carbonal, Vereda Licaligua, Municipio Cácota, Norte de Santander Department, 2400 m alt., 5 Oct 1988, M. R. Campos: 8 males, cb. 23.8, 23.4, 23.1, 22.7, 22.0, 21.6, 19.8, 19.1 mm, cl. 15.0, 14.6, 14.5, 14.2, 13.5, 13.3, 12.7, 12.1 mm; 5 females, cb. 25.6, 21.0, 20.7, 19.5, 16.9 mm, cl. 16.1, 13.8, 13.7, 13.0, 10.8 mm (ICN-MHN-CR 0913). Quebrada Catatumbo, Vereda Licaligua, Municipio Cácota, Norte de Santander Department, 2350 m alt., 5 Oct 1988, M. R. Campos: 8 males, cb. 18.5, 16.7, 16.5, 16.4, 13.9, 12.9, 12.5, 12.0, cl. 12.3, 10.7, 10.6, 10.5, 9.2, 8.7, 8.3, 7.9 mm; 5 females, cb. 25.2, 24.0, 16.7, 15.6, 13.6 mm, cl. 15.0, 14.3, 10.7, 10.3, 9.2 mm (ICN-MHN-CR 0914). Sitio El Naranjal, Vereda Licaligua, Municipio Cácota, Norte de Santander Department, 2250 m

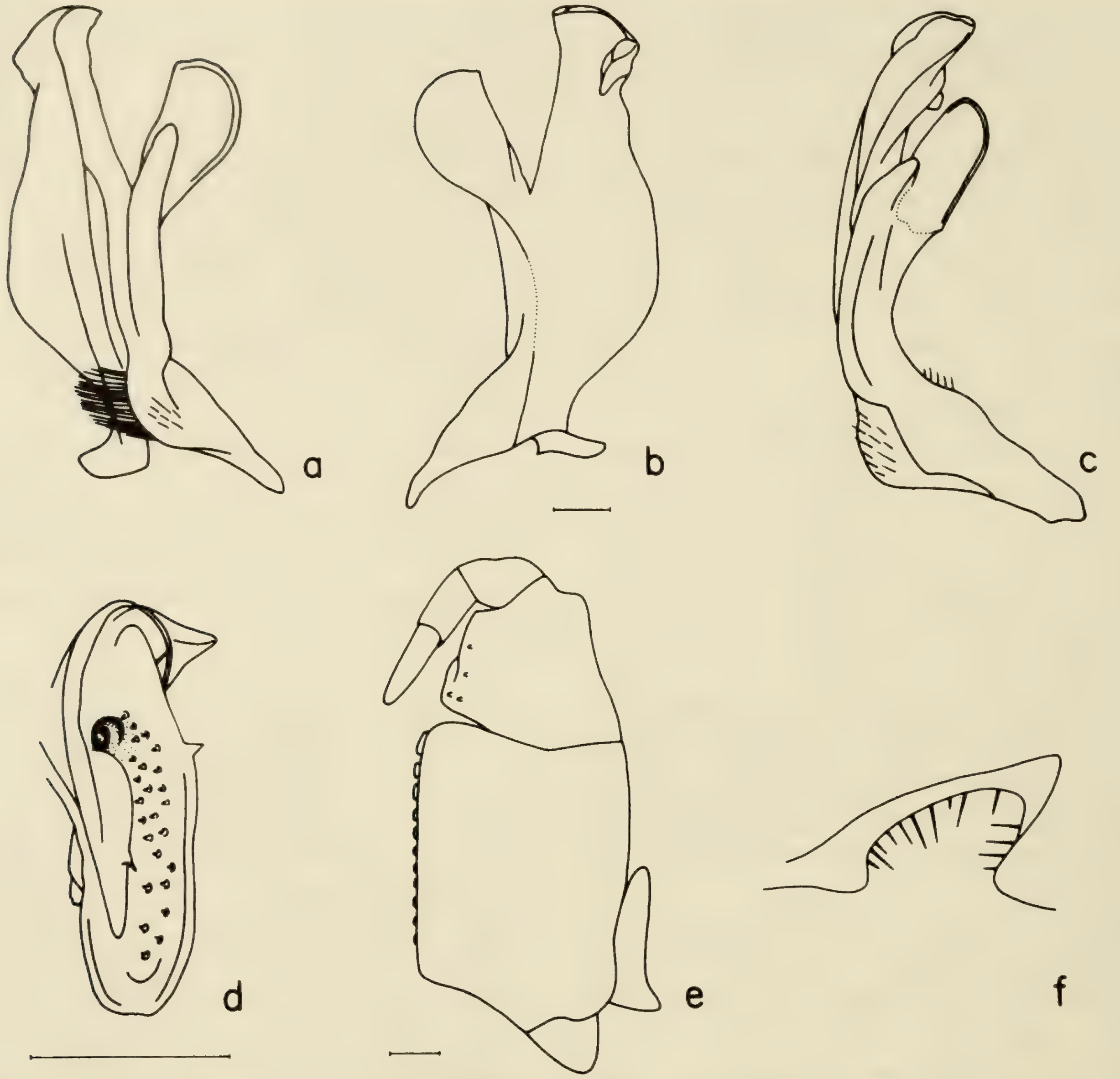

Fig. 5. *Neostrengeria macarenae,* new species, holotype, ICN-MHN-CR 0758: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

alt., 5 Oct 1988, M. R. Campos: 7 males, cb. 26.7, 26.3, 15.8, 15.6, 15.0, 14.7, 14.6 mm, cl. 16.7, 15.7, 10.3, 10.2, 10.1, 10.0, 9.9 mm; 7 females, cb. 28.5, 26.6, 17.5, 14.6, 14.0, 13.0, 12.0, cl. 16.9, 16.4, 11.3, 9.5, 9.4, 8.8, 7.5 mm (ICN-MHN-CR 0915). Vereda Puente López, Municipio Cácota, Norte de Santander Department, 1950 m alt., 5 Oct 1988, M. R. Campos: 1 male, cb. 23.4 mm, cl. 14.8 mm (ICN-MHN-CR 0916). Quebrada La Batea, Vereda Negavita, Municipio Pamplona, Norte de Santander Department, 2200 m alt., 6 Oct 1988, M. R. Campos: 14 males, cb. 23.8, 23.6, 23.4, 22.6, 22.5, 22.2, 22.1, 21.7, 21.4, 20.9, 20.7, 20.5, 20.4, 19.6 mm, cl. 14.2, 14.1, 13.9, 13.5, 13.5, 13.3, 13.2, 13.0, 13.0, 12.9, 12.6, 12.5, 12.4, 12.2 mm; 12 females, cb. 26.2, 23.0, 22.3, 22.2, 22.1, 22.0, 21.8, 21.7, 21.1, 20.4, 20.1, 18.9 mm, cl. 15.6, 13.9, 13.8, 13.5, 13.5, 13.4, 13.4, 13.3, 13.2, 13.1, 12.9, 11.9 mm (ICN-MHN-CR 0917). Sitio Moralitos, Vereda Negavita, Municipio Pamplona, Norte de Santander Department, 2100 m alt., 6 Oct 1988; M. R. Campos: 7 males, cb. 27.6, 27.5, 27.1, 25.0, 21.9, 21.0, 19.2 mm, cl. 16.5, 16.3, 16.2, 15.0, 13.5, 13.2, 12.2 mm; 19 females, cb. 31.5,

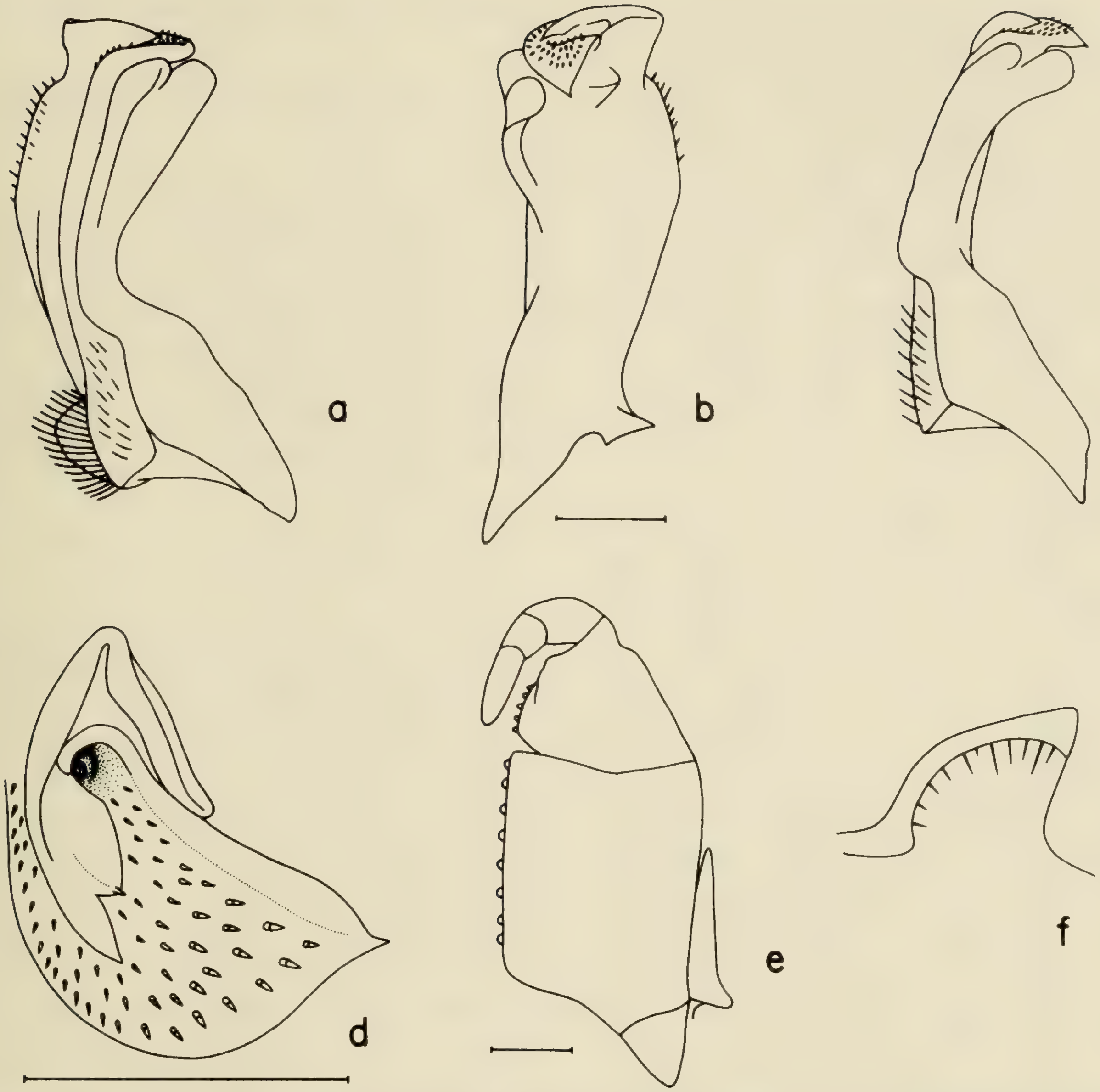

Fig. 6. *Neostrengeria tencalanensis,* new species, holotype, ICN-MHN-CR 0919: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

31.2, 31.1, 29.9, 29.9, 29.5, 28.9, 28.8, 27.7, 26.5, 25.9, 25.5, 23.5, 22.9, 22.6, 22.3, 21.7, 21.4, 21.3 mm, cl. 18.6, 18.5, 18.3, 17.8, 17.8, 17.7, 17.6, 17.6, 16.4, 16.1, 15.7, 15.4, 14.8, 14.5, 14.4, 13.7, 13.5, 13.4, 13.3 mm (ICN-MHN-CR 0918). Sitio Pueblo Nuevo, Vereda San Josecito, Municipio Labateca, Norte de Santander Department, 1600 m alt., 6 Oct 1988, M. R. Campos: 1 male, cb. 19.2 mm, cl. 11.7 mm (ICN-MHN-CR 0920). Sitio Tierra Linda, Vereda Tane, Municipio Chitagá, Norte de Santander Department, 2150 m alt., 7 Oct 1988, M. R. Campos: 1 male, cb. 18.3 mm, cl. 11.5 mm; 2 females, cb. 29.1, 25.2 mm, cl. 17.5, 15.0 mm (ICN-MHN-CR 0921). Vereda Los Llanitos, Municipio Cácota, Norte de Santander Department, 1850 m alt., 7 Oct 1988, M. R. Campos: 2 males, cb. 24.6, 21.3 mm, cl. 14.9, 12.9 mm; 2 females, cb. 23.0, 20.3 mm, cl. 14.3, 13.1 mm (ICN-MHN-CR 0922).

Diagnosis.—Male gonopod with apical portion expanded, forming acuminate projection, covered by a patch of wide, dark spines. Mesial border with strong, short, brown spines and rows of spinulae on distal portion of margin.

Description. —Carapace with cervical groove straight and deep, shallow in posterior half, ending near lateral margin. Anterolateral margin with shallow depression behind orbit, followed by series of papillae on anterolateral half; posterior half smooth. Postfrontal lobes small and ill defined. Median groove absent. Front with upper border ill defined in frontal view, straight with slight middle depression in dorsal view; lower margin slightly sinuous in frontal view. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions well defined.

Palm of larger chela strongly inflated, fingers strongly gaping; palm of smaller chela moderately inflated, fingers not gaping. Distal half of palm and fingers each with small, dark papillae loosely arranged in rows. Walking legs each with 5 rows of large spines on dactylus, spines diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anterolateral and anteroventral rows with 5 spines plus 1 proximal papilla, external row with 5 spines plus 1 pair of proximal papillae, posteroventral and posterolateral rows with 4 spines. Merus of third maxilliped with sharp angle on distal half of external margin; exognath of third maxilliped 0.62 length of ischium (Fig. 6e). Orifice of efferent branchial channel open (Fig. 6f).

Male gonopod narrow in caudal view, with mesial border strongly arched, distal portion wide, with deep recess. Mesial border with strong, short, brown spines and rows of spinulae on distal portion of margin. Accessory lobe elongated, narrow, slightly shorter than lateral lobe and overlapping distolateral border of gonopod in caudal view. Lateral lobe narrow, elongated and bent in cephalic direction, separated from accessory lobe by deep notch (Fig. 6a, b, c). Apical portion expanded, forming acuminate projection, covered by a patch of wide, dark spines. Mesial lobe rudimentary represented by subterminal rough swelling. Projection of spermatic channel bifid, with a spinule and small ridge on inner side (Fig. 6d).

Etymology. —The specific name refers to the town of Tencalá, where the type was collected.

Remarks. —This species resembles *Neostrengeria lobulata* in the shape of the male gonopod, but in *N. lobulata* the accessory lobe is wider on distal portion, the distolateral margin carries a characteristic bulbous projection covered by a patch of spines and the apical portion is surrounded by a wider irregular expansion.

Neostrengeria tonensis, new species

Fig. 7

Material examined. —Vereda Caragua, Bucarmanga-Cucuta highway, Municipio Tona, Santander Department, 1700 m alt., 25 Mar 1987, M. R. Campos: 1 male holotype, cb. 26.0 mm, cl. 15.2 mm; 5 male paratypes, cb. 23.4, 22.1, 22.0, 19.9, 19.1 mm, cl. 13.8, 13.2, 13.2, 12.2, 11.5 mm; 6 female paratypes, cb. 21.8, 21.4, 21.3, 20.2, 20.0, 19.0 mm, cl. 12.5, 12.3, 12.2, 11.8, 12.0, 10.6 mm (ICN-MHN-CR 0687). Inspección La Corcova, Bucaramanga-Cúcuta highway, Municipio Tona, Santander Department, 2400 m alt. 25 Mar 1987, M. R. Campos: 4 males, cb. 22.5, 21.6, 20.3, 18.8 mm, cl. 14.2, 13.3, 12.5, 11.8 mm; 6 females 26.1, 24.9, 24.4, 22.9, 22.4, 21.8 mm, cl. 15.7, 15.2, 15.0, 13.9, 13.6, 13.5 mm (ICN-MHN-CR 0689-0690). Estación La Mariana, Inspección La Corcova, Municipio Tona, Santander Department, 2150 m alt., 31 Mar 1987, M. R. Campos: 4 males, cb. 21.8, 17.1, 15.5, 14.7 mm, cl. 13.4, 10.6, 9.8, 9.5 mm; 2 females, cb. 16.6, 16.5 mm, cl. 10.5, 10.3 mm (ICN-MHN CR 0709).

Diagnosis. —Male gonopod with accessory lobe widely spatulated, rounded distally, as long as lateral lobe, separated by shallow notch from lateral lobe. Apical portion oval, with conspicuous and wide spine.

Description. —Carapace with cervical groove straight and deep, not reaching lat-

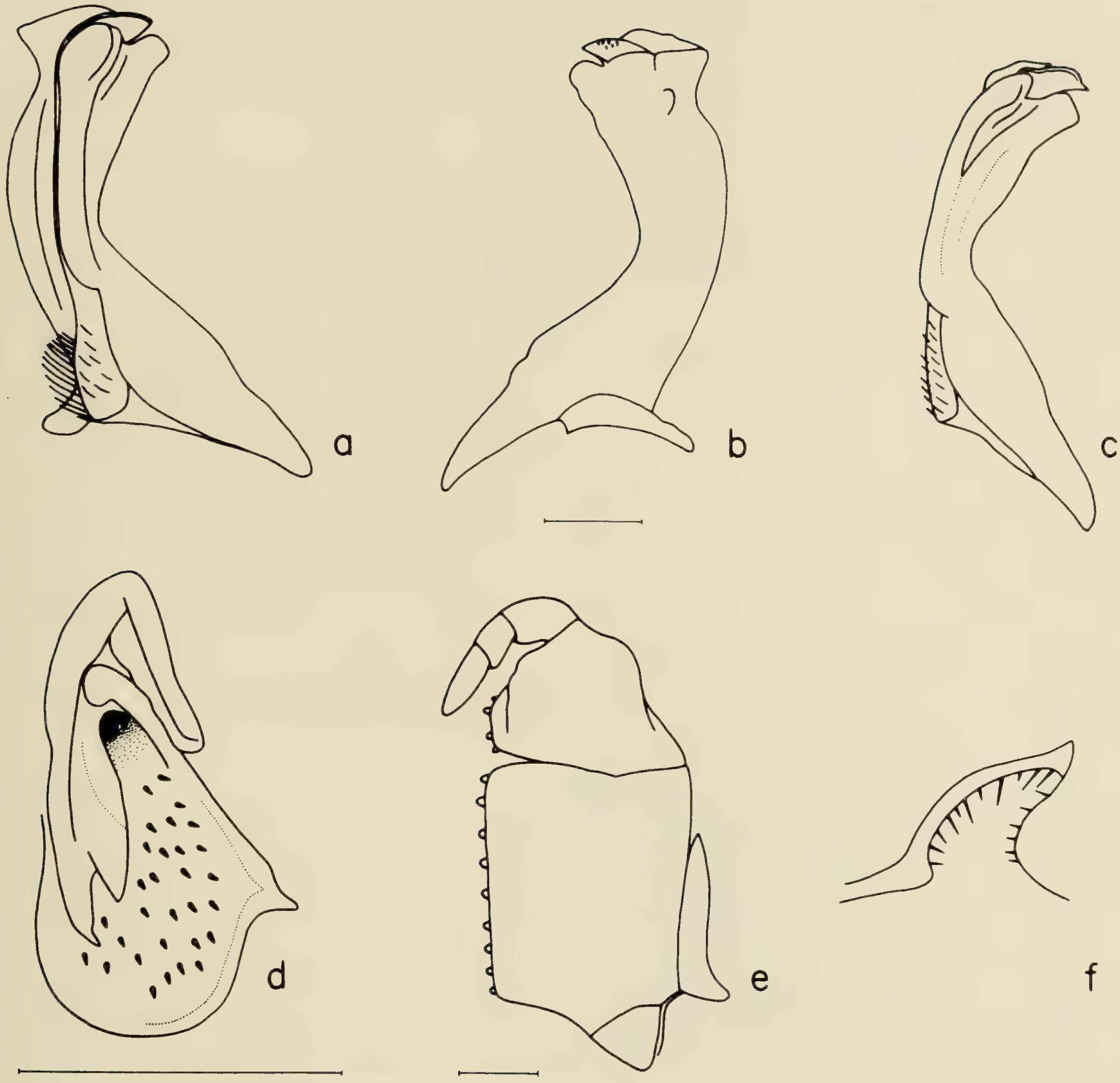

Fig. 7. *Neostrengeria tonensis,* new species, holotype, ICN-MHN-CR 0687: a, Left gonopod, caudal view; b, Mesial view of same; c, Lateral view of same; d, Apex of same in distal view; e, Third maxilliped; f, Left opening of branchial channel. Scales equal 1 mm.

eral margin. Anterolateral margin with shallow depression behind orbit, followed by series of ill defined papillae. Postfrontal lobes low, their presence indicated only by 2 small scars. Median groove absent. Front with upper border ill defined in frontal view, convex, with slight depressions at middle in dorsal view; lower margin strongly sinuous in frontal view; carapace moderately inclined anteriorly behind front. Lower orbital margin with row of tubercles. Surface of carapace smooth, covered by small papillae; regions well defined.

Palm of larger chela strongly inflated; fingers gaping; palm of smaller chela moderately inflated, fingers not gaping. Walking legs each with 5 rows of spines on dactylus; spines conspicuous, diminishing in size proximally. Arrangement of spines over dactylus of third left pereiopod as follows: anteroventral row with 5 spines, anterolateral row with 5 spines plus 1 proximal papilla, external row with 4 spines plus 1 pair of proximal papillae and 4 intercalated papillae, posteroventral row with 5 spines, and posterolateral row with 3 spines plus 1 proximal papilla. Merus of third maxilliped with a shallow depression on distal half of ex-

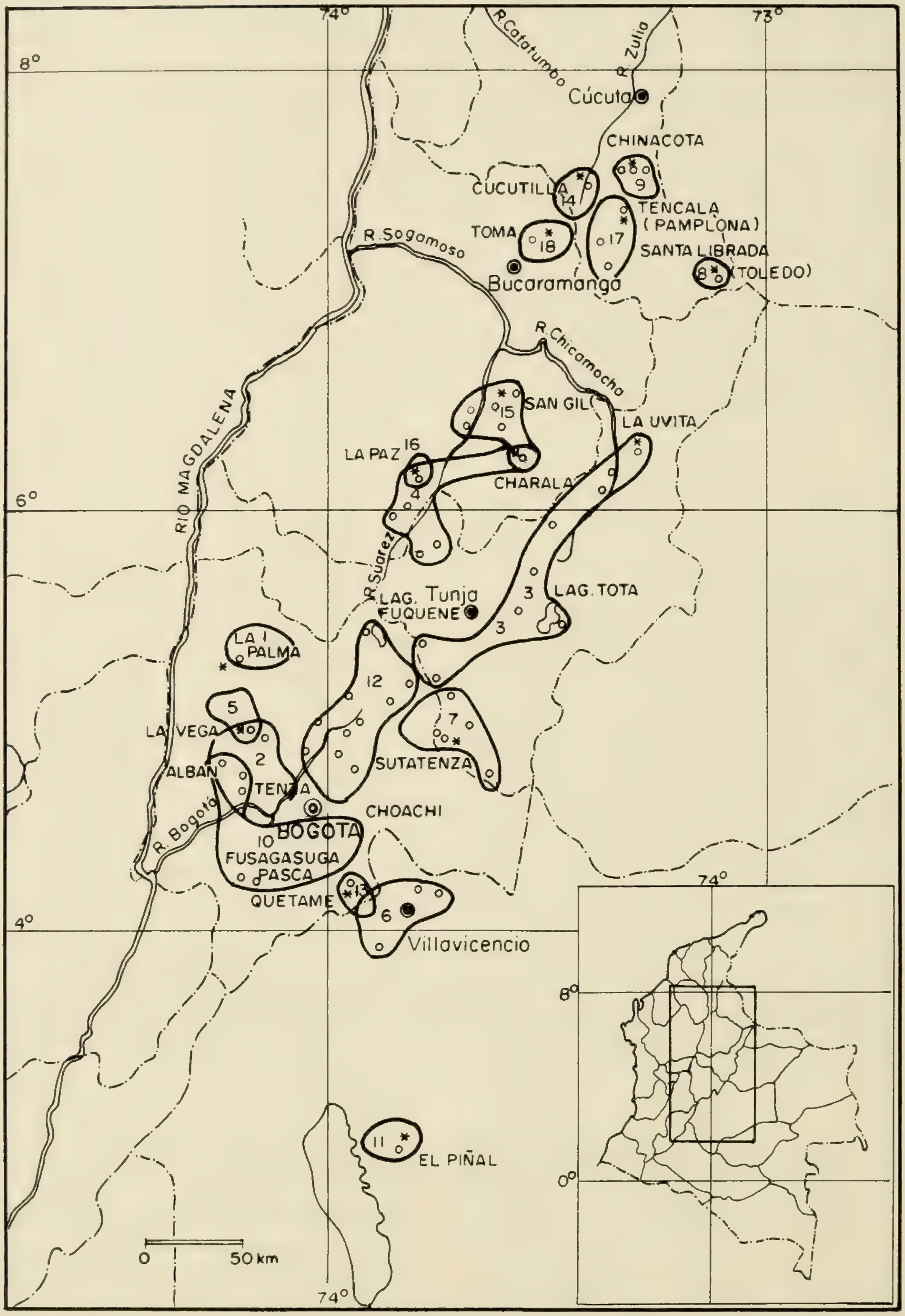

Fig. 8. Map of the Eastern Cordillera, Colombia, showing the distribution of the species of *Neostrengeria*: 1, *N. aspera*; 2, *N. botti*; 3, *N. boyacensis*; 4, *N. charalensis*; 5, *N. gilberti*; 6, *N. guenteri*; 7, *N. lasallei*; 8, *N. libradensis libradensis*; 9, *N. libradensis appressa*, 10, *N. lindigiana*; 11, *N. macarenae*; 12, *N. macropa*; 13, *N. monterrodendoensis*; 14, *N. lobulata*; 15, *N. niceforoi*; 16, *N. sketi*; 17, *N. tencalanensis*; 18, *N. tonensis*. Open circles indicate localities; asterisks indicate type localities; overlapped areas indicate sympatric regions.

ternal margin; exognath of third maxilliped 0.66 times length of the ischium (Fig. 7e). Orifice of efferent branchial channel open (Fig. 7f).

Male gonopod narrow in caudal view, with mesial border strongly arched, distal portion wide, with deep recess. Accessory lobe widely spatulated, rounded distally, as long as lateral lobe, separated by shallow notch from lateral lobe, and overlapping distolateral border of gonopod in caudal view. Lateral lobe narrow, elongated and bent in cephalic direction (Fig. 7a, b, c). Apical portion oval, with conspicuous and wide spine. Mesial lobe rudimentary, represented by subterminal rough swelling. Projection of spermatic channel, with a spinule on inner side (Fig. 7d).

Etymology.—The specific name refers to the Municipio Tona, where the type was collected.

Remarks.—This species resembles *Neostrengeria tencalanensis* in the shape of the male gonopod, but in N. *tencalanensis* the accessory lobe is narrower, the apical portion expanded, forming acuminate projection, covered by a patch of wide, dark spines and the mesial border with strong, short, brown spines and rows of spinulae on distal portion of margin.

Distribution of the Species

The new species described extend the knowledge of the genus *Neostrengeria,* which now comprises 18 species distributed on the slopes and high plain of the Eastern Cordillera of the Andes in Colombia (3°–7°40′N and 73°–74°15′W). The area of distribution is limited by the region of Bochalema (Norte de Santander Department) to the north, by the Tena region (Cundinamarca Department) to the west, and by the Serranía de la Macarena (Meta Department) to the south (Fig. 8), with altitudes ranging from 400 to 3000 m above sea level.

The species *Neostrengeria gilberti, N. niceforoi, N. aspera, N. sketi, N. charalensis, N. botti* and *N. tonensis* are distributed on the western slope of the cordillera, while *N. macarenae, N. guenteri, N. monterrodendoensis, N. libradensis appressa, N. libradensis libradensis, N. lasallei, N. tencalanensis* and *N. lobulata* are encountered on the eastern slope. *Neostrengeria lindigiana* is found on both slopes, and *N. macropa* and *N. boyacensis* occur on the high plain of this mountain range.

Species of the genus are found in watersheds of the Magdalena, Orinoco and Catatumbo rivers. *N. lindigiana, N. botti, N. gilberti, N. aspera, N. macropa, N. boyacensis, N. charalensis, N. sketi, N. niceforoi* and *N. tonensis* are found in the Magdalena River watershed; *N. macarenae, N. guenteri, N. monterrodendoensis, N. lasallei* and *N. libradensis libradensis* on the Orinoco River watershed, whereas *N. lindigiana* occurs in both of these watersheds. *N. lobulata, N. tencalanensis* and *N. libradensis appressa* are restricted to the Catatumbo River basin in the northern region of distribution.

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A NEW CRETACEOUS CRAB, *DIAULAX MILLERAE* (CRUSTACEA: DECAPODA), FROM THE NORTHERN ATLANTIC COASTAL PLAIN, U.S.A.

Gale A. Bishop

Abstract.—Two specimens representing a new species, *Diaulax millerae,* of a Cretaceous crab were collected from spoil banks of the Chesapeake and Delaware Canal from the lower Campanian Merchantville Formation. The new species is characterized by a hexagonal, relatively flat carapace with moderately developed grooves and prominent tubercles on the epibranchial dorsal shield margins. The specimens are preserved as internal carapace steinkerns enclosed in apatite concretions associated with numerous decapods of the Chesapeake and Delaware Canal Assemblage. The description of *D. millerae* extends the stratigraphic range of *Diaulax* from the Early Cretaceous into the Late Cretaceous. Review of the stratigraphic and geographic distribution of *Diaulax* shows a possible pattern of development along the northern margin of the Tethys Seaway in Texas followed by an eastern migration into Great Britain during the Early Cretaceous, then immigration into the opening Atlantic during the Late Cretaceous.

The apatite-preserved, decapod-rich fauna of the Merchantville Formation from the Chesapeake and Delaware Canal described by Roberts (1962) consists of six taxa of lobsters, two thalassinoid taxa, one hermit crab taxon, and eleven taxa of brachyuran crabs found in association with abundant invertebrates:

Lobsters

Enoploclytia sp.
Hoploparia gabbi Pilsbry, 1901
Hoploparia gladiator Pilsbry, 1901
Oncopareia sp.
Archaeocarabus? *whitfieldi* (Pilsbry, 1901)
Linuparus richardsi Roberts, 1962

Hermit Crabs

Palaeopagurus pilsbryi Roberts, 1962

Burrowing Shrimp

Protocallianassa mortoni (Pilsbry, 1901)
Protocallianassa praecepta Roberts, 1962

Crabs

Raninella tridens Roberts, 1962
Notopocorystes testacea (Rathbun, 1926)
Homolopsis atlantica Roberts, 1962
Homolopsis dispar Roberts, 1962
Tetracarcinus subquadratus Weller, 1905
Necrocarcinus rathbunae Roberts, 1962
Paranecrocarcinus gamma Roberts, 1962
Prehepatus dilksi Roberts, 1962
Xanthosia elegans Roberts, 1962
Xanthias? *lenolensis* Rathbun, 1935

Collecting in the spoil piles of the Chesapeake and Delaware Canal during canal construction in the early 1970's led to the accumulation of abundant, beautifully preserved specimens designated herein as the Merchantville Chesapeake and Delaware

Assemblage. Two specimens, collected in the 1970's by Cynthia Miller and William Beck which are not assignable to any existing taxon, are described herein and named *Diaulax millerae.* They were transmitted to me for study by Harry Mendryk. The Chesapeake and Delaware Decapod assemblage represents the preserved fraction of a decapod association which existed on the Northern Atlantic Coastal Plain during mid-early Campanian time (Owens et al. 1970:32).

The decapod portion of the Merchantville fauna from the Chesapeake and Delaware Canal consists of approximately 2000 specimens. The low rate of incidence of *D. millerae* (abundance of 0.1%) in the Merchantville Chesapeake and Delaware Canal Assemblage indicates the probability of collecting additional specimens of this species will be very small. The description of *D. millerae* increases the completeness of the North American record for *Diaulax* (Glaessner 1969).

Type specimens of the new species are deposited in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (USNM).

Systematic Paleontology

Section Podotremata Guinot, 1977
Subsection Dromiacea de Haan, 1833
Family Diaulacidae Wright & Collins, 1972
Genus *Diaulax* Bell, 1863

Type species.—*Diaulax carteriana* Bell, 1863 (=*Platypodia oweni* Bell, 1850) is cited as the type species by monotypy (Wright & Collins 1972).

Diagnosis.—Carapace more or less hexagonal, length more or less equal to width, widest at anterior ⅓, moderately arched longitudinally, especially anteriorly; transversely flat; lobes somewhat tumid, moderately differentiated; cervical and branchiocardiac grooves weakly developed, transverse; front generally downturned; lateral margins sharply reflexed, ornamented by small spines, slightly convergent posteriorly; posterior margin convex, bordered by broad groove. Rostrum pointed or squared, downturned, may be sulcate with edges turned upward into lobes; orbits small.

Discussion.—*Diaulax* is known from the Lower Cretaceous (lower Albian) Glen Rose Limestone of central Texas, from the Lower Cretaceous (middle and upper Albian to lower Cenomanian) of Great Britain, and, with the description of *D. millerae,* its range is extended into the Upper Cretaceous of North America (mid-lower Campanian of the Northern Atlantic Coastal Plain). The assignment of this taxon to *Diaulax,* necessitating an emendation of the generic diagnosis, constituted a conservative taxonomic approach taken instead of creating a new genus-level taxon. This action was necessary because *D. millerae* is longer than wide rather than wider than long. Relative carapace width and length is a characteristic which is judged to be easily changed in the evolution of brachyurans.

Diaulax millerae, new species
Fig. 1

Synonymy.—*Diaulax* sp., Bishop 1986, p. 133.

Diagnosis.—Carapace more or less hexagonal, longer than wide, widest near ends of cervical groove; longitudinally flat, somewhat downturned anteriorly, moderately to poorly grooved with weak cervical and branchiocardiac grooves; lateral margins convergent posteriorly; regions smooth to finely granulate, non-tumid.

Types.—Holotype (USNM 462295) and paratype (USNM 462296).

Occurrence and preservation.—Specimens of *Diaulax millerae,* preserved as internal steinkerns enclosed in apatite concretions, with some appendages visible on the surface of the concretions, were collected on construction dredge spoils at the Chesapeake and Delaware Canal, Newcastle County, Delaware. These spoil piles were produced during construction of a new canal section and are from the Merchantville Formation.

Description.—Carapace hexagonal, longer (18.2 mm) than wide (14.1 mm), widest just anterior to ends of cervical groove approximately 0.40 the distance from the front. Anterior margin convex, rostrum produced anteriorly beyond orbits, sulcate with mesial ridge, bilobed; anterolateral margins rounded to widest part anterior to intersection with cervical groove; lateral margins broadly rounded, somewhat straighter posterior to cervical groove, convergent posteriorly; posterolateral edge somewhat sinuous angular; posterior margin sinuous, concave at middle, bordered by narrow rim. Dorsum relatively flat, regions (as defined by Wright & Collins 1972: fig. 1) poorly delineated by broad, shallow grooves. Cervical groove discontinuous across gastric region, moderately incised from gastric ridge to edge of dorsum, not visible across gastric ridge, separating the dorsum into an anterior portion (cephalic arch of Milne-Edwards as defined by Bell 1858, iii) and a posterior portion (scapular arch of Milne-Edwards as defined by Bell 1858, iii). Groove delineating mesogastric very shallow and poorly defined, sweeping backward and outward from the rostrum, nearly joining cervical groove. Branchiocardiac groove broad and shallow, transverse and somewhat sinuous, rather deeply incised across sagittal ridge where it splits, one branch reflexed sharply anteriorly and distally to form broad depression oriented as if to join junction of mesogastric and cervical grooves, the other branch looping posteriorly, then outward around epimeral peninsula, again splitting with another branch bounding anterior and lateral margins of the cardiac lobe and nearly coming together at posterior of cardiac lobe. Epimeral peninsula raised and continuous with narrow, but prominent, ridge immediately posterior to transverse branch of branchiocardiac groove.

Cephalic arch (as used by Milne-Edwards as defined by Bell 1858, iii) broad and bulbous; faintly differentiated by mesogastric grooves into mesogastric and large distal epigastric-protogastric-hepatic regions; epigastric regions faintly produced into raised bosses; hepatic and protogastric regions somewhat differentiated by broad, shallow hepatic depression [=hepatic groove]. Mesogastric lobe with long, narrow anterior tongue extending onto the rostral area which is apparently downturned into a bifurcated rostrum, gradually widening posteriorly to triangular mesogastric lobe. Orbits well defined, 47.2% of carapace width, inner and outer orbitals separated by narrow, sharp, granulate inner rim; outer orbital margin ringed by narrow, granulate rim, terminating in prominent extraorbital projection at outermost angle.

Scapular arch delimited by shallow furrows into gastric region and branchial lobes. Gastric ridge barely differentiated by cervical furrow between mesogastric and urogastric lobes, well defined by branchiocardiac groove. Cardiac region distinct, separated from urogastric lobe by broad groove, somewhat keyhole-shaped, with 3 tubercles arranged in isosceles triangle, base anterior. Branchial region differentiated into small, anterior epibranchial-mesobranchial region and large, posterior metabranchial region. Mesobranchial region only faintly separated from distal epibranchial region by very shallow groove splitting off cervical groove. Epibranchial region inflated and angular, forming epibranchial angle and widest portion of carapace accentuated by curvature of cervical furrow around a moderately-sized epibranchial spine on the dorsal edge. Mesobranchial region forms a somewhat sinuous transverse ridge. Metabranchial region mostly flat but with narrow, prominent ridge and broad depression anteriorly.

Pterygostomial region wide and tightly reflexed beneath carapace; mouth frame with straight, subparallel margins raised into narrow rim, diverging posteriorly to meet

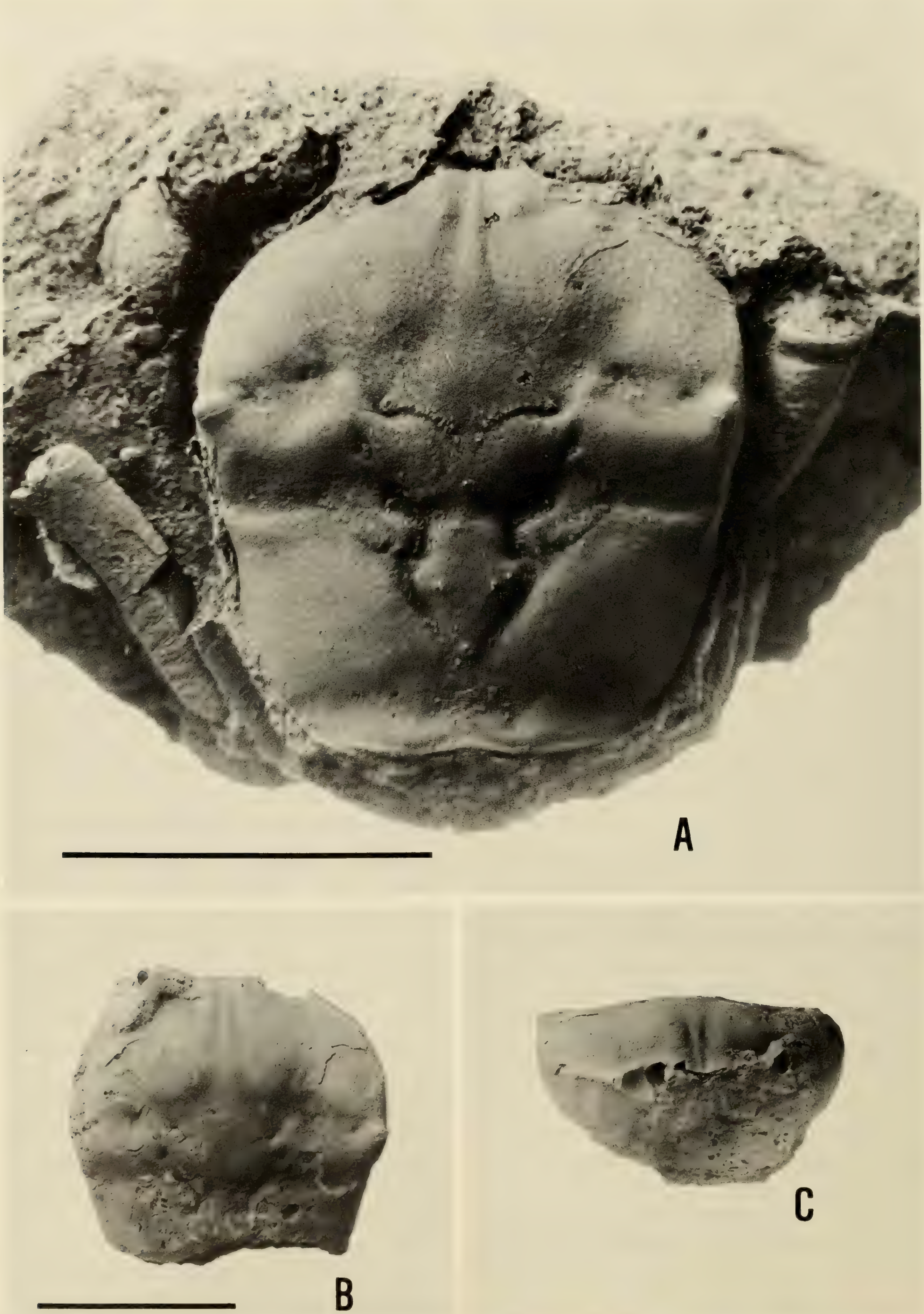

Fig. 1. Photographs of *Diaulax millerae,* new species, embedded in concretion; A. Dorsal view of holotype, B. Dorsal view of paratype, C. Anterior view of paratype. (Scales = 1 cm.)

sternum. Pterygostomial region with two subparallel depressions, the anterior-most sweeping in from dorsal shield edge and continuous with transverse branch of branchiocardiac groove, the other short and not continuous to dorsal shield edge or mouth frame. Pleural suture follows anterior-most groove for about 0.66 of its distance from front to back. The cervical furrow becomes obsolete at the dorsal shield edge on the upper surface of the carapace, but its position can be traced by its smoothness relative to the finely granulate surface of the rest of the pterygostomial region. It enters the pterygostomial region just anterior to the epigastric spine, runs parallel to the extension of the branchiocardiac groove to the middle of the pterygostomial region where it splits, one branch rising to the anterolateral edge of the dorsal shield and the other running to the extension of the branchiocardiac groove.

Chelipeds approximately equal; merus stout; carpus pentagonal, moderately sized; propodus short and high, strongly granulate (at least on inner face); dactylus long, narrow, and strongly curved downward. Pereiopods 2 and 3 have stout meri; other thoracopods unknown.

Etymology.—This species is named in honor of Cynthia Miller who collected the holotype.

Comparison.—*Diaulax millerae* is easily distinguished from its North American congenor *Diaulax roddai* Bishop 1983, by its difference in outline which is sub-hexagonal rather than kite-shaped as in *D. roddai,* by the anterior margin lacking the prominent extraorbital angles of *D. roddai,* by having an inflated and rounded cephalic arch which is inflated and rounded rather than flat and somewhat depressed as in *D. roddai,* and by differences in ornament including prominent epibranchial tubercles which are lacking in *D. roddai. D. millerae* is similar in carapace outline to *D. oweni* (Bell 1850) but differs by being longer, by having less tumid lobes, and more rounded anterolateral margin not interrupted by anterolateral spines as in *D. oweni. D. millerae* differs even more from *D. feliceps* Wright & Collins 1972, in outline, being relatively much longer, and in differences in the shape of the cervical and branchiocardiac grooves, and by having a rounded anterolateral margin rather than straighter deeply invaginated anterolateral margins of *D. feliceps.*

Remarks.—The preservation of a fossil such as *D. millerae* does not present the complete complement of morphologic information, particularly on the exterior surface of the cuticle and the distal parts of the appendages, however the gross morphology preserved is adequate to define this new taxon. The complete description of this crab's morphology must await additional specimens found with preserved exoskeleton and appendages. The presence of *D. millerae* in the Chesapeake and Delaware Canal Merchantville Decapod Assemblage reemphasizes the need for large collections of decapods from apatite-preserved decapod-rich assemblages. Only collections consisting of hundreds or thousands of decapods are likely to have a significant chance of yielding scarcer faunal elements such as *D. millerae.*

Paleogeography and Biostratigraphy of *Diaulax*

The pattern of evolution of *Diaulax* is one of initial derivation from ancestral stock in the Jurassic in Central and Northern Europe (Glaessner 1931:4; Wright & Collins 1972: 55), emigration and adaptive radiation in the shallow waters of the northern Tethys in Texas and southern England, followed by emigration and speciation in the opening Atlantic on the Northern Atlantic Coastal Plain. The species assignable to the genus *Diaulax* show an interesting pattern of development and evolution indicating an origin in the northern Tethys Seaway in the Early Cretaceous possibly, migration and evolution in the shallow waters of the northern Tethys in southern Great Britain (*D. oweni* Bell 1850, and *D. feliceps* Wright & Collins 1972), then migration and evolution

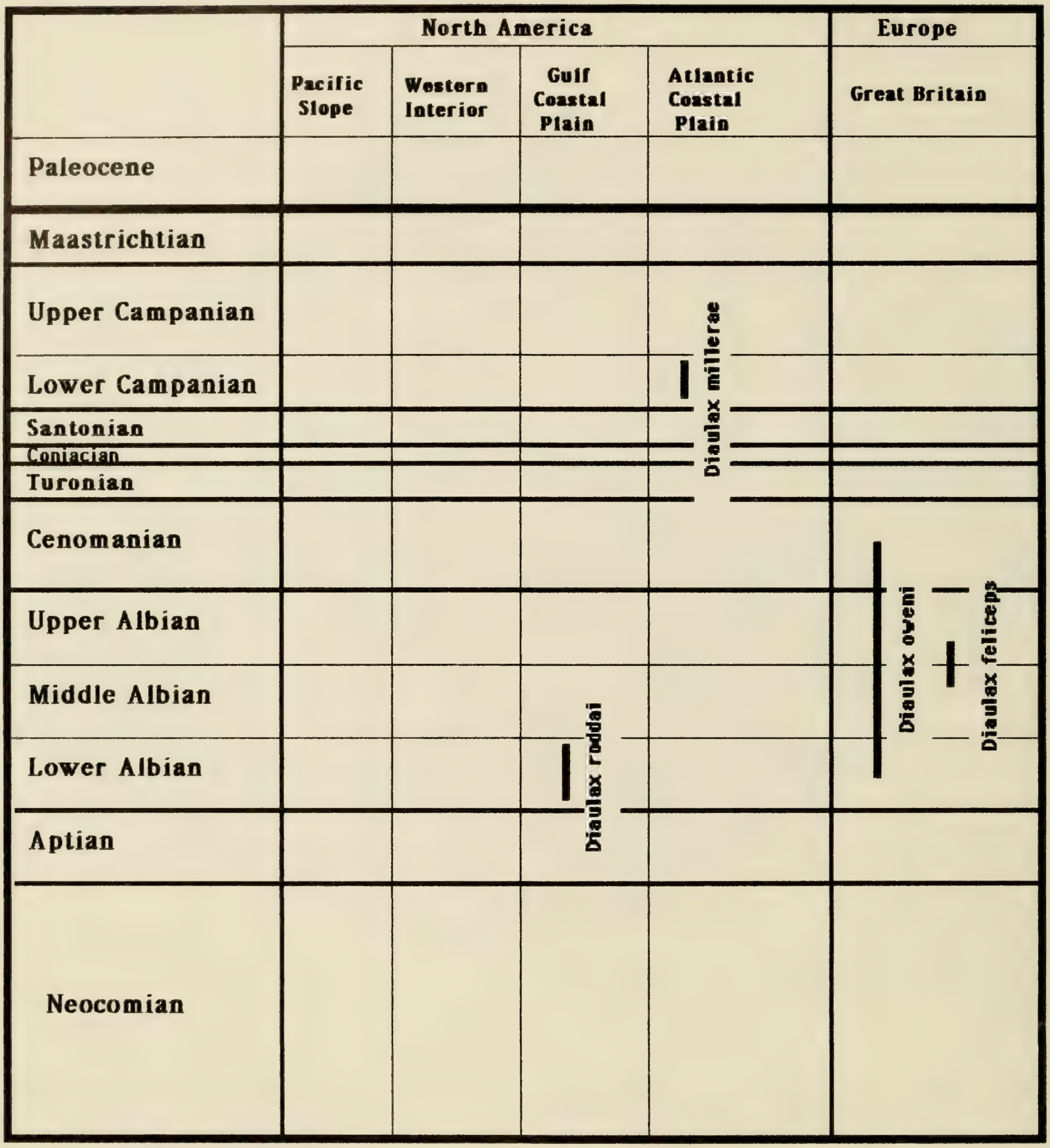

Fig. 2. Stratigraphic sequence and approximate geographic position of described species of *Diaulax*.

on the Northern Atlantic Coastal Plain (*D. millerae*, new species). Carter (1898:20), and subsequently Wright & Collins (1972), cite the existence of a yet unsubstantiated, undescribed species of *Diaulax* from the Oligocene or Miocene of England.

Acknowledgments

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REDESCRIPTION OF THE HIPPOLYTID SHRIMP *TRACHYCARIS RUGOSA* (BATE) (CRUSTACEA: DECAPODA: CARIDEA) FROM THE WESTERN ATLANTIC, WITH NOTES ON SEXUAL DIMORPHISM

Maria M. Criales

Abstract.—*Trachycaris rugosa* (Bate, 1888) is redescribed and figured based on specimens from the western Atlantic. This species shows a remarkable sexual dimorphism in size, shape and length of the rostrum, abdominal pleura, ventromedian abdominal spines, and antennular peduncle. *Trachycaris rugosa* differs from the eastern Atlantic *Trachycaris restricta* (A. Milne Edwards, 1878) in the absence of a palp on the mandible, the presence of two spines on the basal antennal peduncle, and a two-segmented palp on the first maxilliped.

While examining material of *Trachycaris rugosa* (Bate, 1888) from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), to determine the identity of some specimens of *Trachycaris* collected in Santa Marta, Colombia, it was found that, with the exception of one specimen from Bermuda (USNM 351963), the USNM and Santa Marta specimens represent the same species. The specimens agree with the original description of *Trachycaris rugosa* (Bate, 1888), and differ from the eastern Atlantic *T. restricta* Holthuis (1949) in that in the former a palp is absent on the mandible, there are two spines on the antennal peduncle, and the palp of the first maxilliped is two-segmented. Also, considerable sexual dimorphism was found in the specimens of *T. rugosa,* especially reflected in size, shape of the rostrum, abdomen and antennular peduncles.

Total length (TL) of the specimens was measured from the anterior tip of the rostrum to the posterior median margin of the telson, and carapace length (CL) was measured from the tip of the rostrum to the posterior median margin of the carapace.

Although the *Trachycaris* species are typically designated as "*rugosus*" and "*restrictus,*" "*rugosa*" and "*restricta*" will be used in this paper to agree with the feminine *Trachycaris.*

Trachycaris rugosa (Bate, 1888)
Figs. 1–5

Platybema rugosus Bate, 1888:579, pl. 104, fig. 2. [type locality: off Culebra Island, Puerto Rico, depth 390 fm (713.3 m)].
Trachycaris rugosus: Calman, 1906:33.
Trachycaris restrictus: Holthuis, 1949:233, figs. 2–3 (in part, see remarks).

Material examined.—Colombia: 2 ♂, Isla de la Aguja ca. 11°18′N, 74°10′W, 25 m, 8 Aug 1987, on calcareous algae, coll.: B. Werding, USNM 252485; 1 ♀ ovig., Santa Marta, ca. 11°13′N, 74°9′W, 8 m, Feb 1980, sand, coll.: B. Werding, USNM 252485. Barbados: 1 ♀ ovig. Barbados-Antigua Exp., English Harbor 8, USNM 125144.

Virgin Islands: 1 ♀ juv. off St. Thomas, 20 ft (36.6 m), coral, Feb 1899, USNM 24691.

Puerto Rico: 2 ♀ ovig., off Culebra, R/V *Fish Hawk* 15 fm (27.4 m), coral sand, Feb 1899, USNM 24692, 24964; 2 ♀ ovig., off Jallabor Bay, July 1915, USNM 1135, 1179;

2 ♀, Mayaguez, on coral reef, 20 Jan 1899, USNM 24690.

Mexico: 1 ♀ ovig., Yucatan, off Cape Catoche, 22°18′N, 87°04′W, R/V *Albatross,* 24 fm (43.9 m), USNM 23308.

Cuba: 1 ♀, S. of Hicacos, Varadero, 2 Jan 1957, dredge haul, coll W. Schmitt, USNM 213537.

Belize: 1 ♀ ovig., Stann Creek District, Carrie Bow Cay, May 1981, on the alga *Rhipocephalus* sp., USNM 184510.

Gulf of Mexico: 1 ♀ ovig., off Charlotte Harbor 26°33′N, 83°10′W, 28 fm (51.2 m), 2 Apr 1901, sand, R/V *Fish Hawk,* USNM 24693; 2 ♀ ovig. 1 ♀ juv., between 29°14′30″N, 85°32′W and 29°16′N, 85°32′W, R/V *Albatross,* 24–27 fm (43.9–49.4 m), 30 Jan 1885, USNM 23770, 23771, 9599.

Florida Keys: 3 ♀ ovig., 1 ♀ juv., Dry Tortugas, 27 fm (49.4 m), Jan 1925, coll. W. L. Longley, USNM 144662, 127956, 127957, 127958, 2 ♀, S. of Cape San Blas, 29°11′18″N, 85°29′32″W, R/V *Albatross,* 25–27 fm (45.7–49.4 m), 7 Feb 1885, USNM 23769, 2374.

South Carolina: 7 ♂, off S. Carolina, between 31°31′54″N, 78°39′42″W, and 32°49′18″N, 78°49′18″W, between 33–68 m, Aug 1981, suction sampler, USNM 224965, 224966, 224967, 22070, 22071, 224989.

Redescription.—Carapace varying considerably with size and sex (Figs. 1a, b; 2a, b). Rostrum of adult females strongly compressed laterally, approximately as long as high, tip truncated with 5–6 small teeth; lower margin with 3 large teeth, upper margin with 6 or 7 teeth (Fig. 1b). Dorsomedian ridge of carapace sloping sharply down to rostrum, with several teeth distinctly larger than those of rostrum, unequal in size. Adult males with elongate rostrum, approximately twice as long as high, ending in 2 apical teeth, tip truncated with 3–4 small teeth; lower margin with 3 rather large teeth; upper margin with 6 teeth, continuing in relatively straight line to dorsomedian ridge (Fig. 2b). Juveniles of both sexes with carapace similar, different from adults (Figs. 1a, 2a); dorsal ridge rising behind eye and sloping down to rostrum, more pronounced with size in females, tending to be flat in males (Figs. 1b, 2b). Carapace with several tubercles ending in anteriorly directed spines variable in size and location but with following general pattern: behind cervical groove a row of 3–4 spinules, and another 3 or 4 forward (absent in juveniles); row of 4–5 tubercles beginning behind antennal spine and running along lateral surface; under this row another 3–6 tubercles near lateral margin of carapace; near highest point of dorsal ridge there is another group of tubercles variable in number. Adult females with additional group of tubercles near posterolateral margin of carapace. Juveniles with fewer and smaller tubercles. Upper margin of orbit with distinct supraorbital spine, lower angle ending in sharp pterygostomial spine; anterior margin with a strong antennal spine, below which are 3 other small spines on anterolateral angle of carapace (Figs. 1a, b; 2a, b).

Antennular peduncle with basal segment with distinct, large stylocerite, ending in 2 processes. Proximal process tapering into sharp anteriorly directed tip, the other rounded but with distinct spine at the top. Between 2 processes a deep, rounded notch. Ventral surface with strong curved spine directed to outside of peduncle. In males, second segment robust and short about ⅓ length of third. Flagella short, consisting of about 6 articles (Fig. 2d). In females, second segment slightly longer than third, flagella consisting of approximately 8 articles (Fig. 1d).

Antennal scale overreaching antennular peduncle by about ⅓ of its length, about twice as long as broad; outer margin ending in distinct terminal tooth overreaching the lamella. Antennal peduncle bearing 1 small dorsal spine and 2 large ventral spines, largest located near base of scaphocerite, smallest near distal border. Antennal flagellum consisting of 15 or 16 articles (Fig. 3g).

Mandible lacking palp. Molar process with

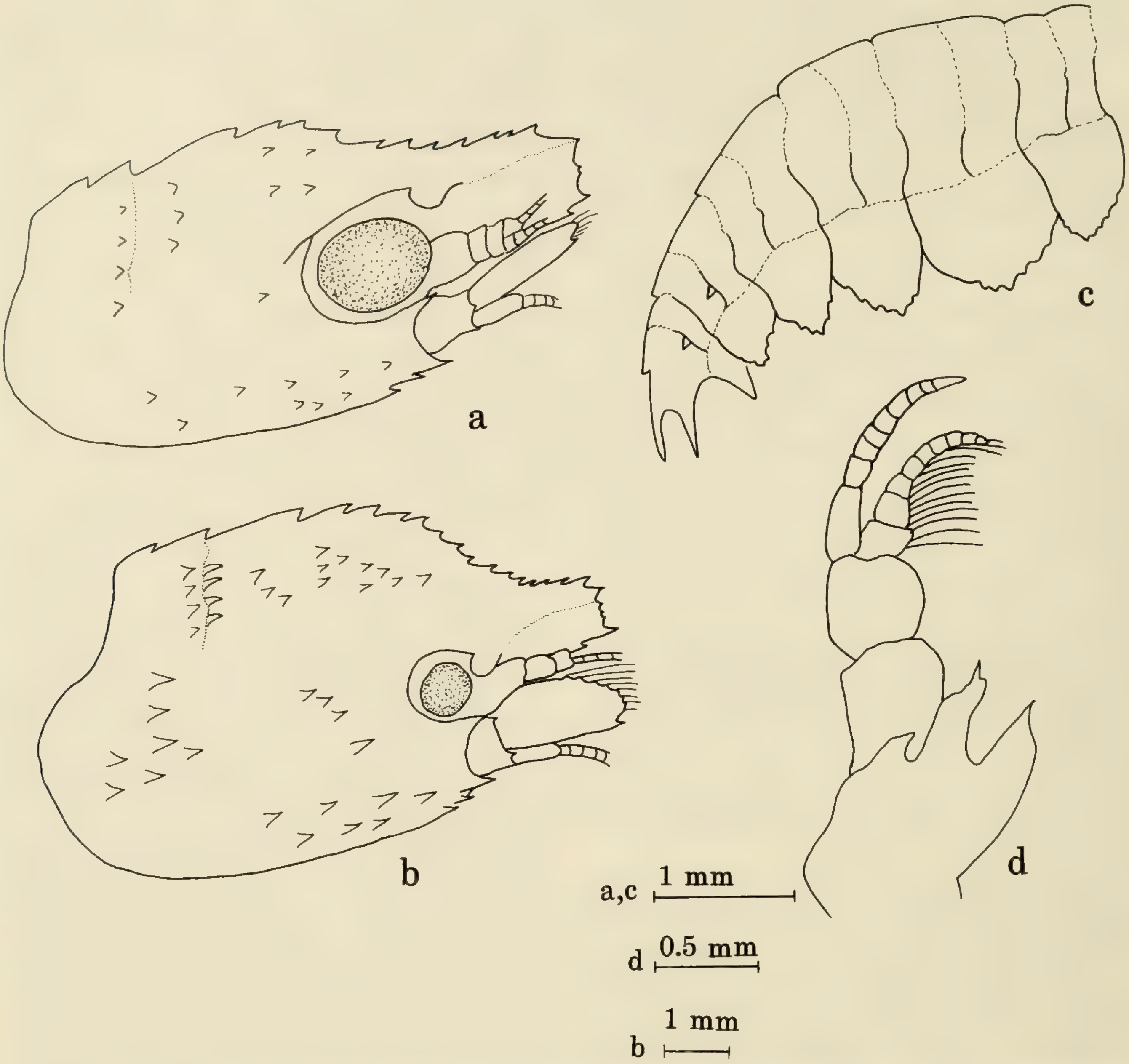

Fig. 1. *Trachycaris rugosa* Bate, females from Puerto Rico (USNM 24691, 1135). a, carapace of juvenile female; b, carapace of adult female; c, abdomen of juvenile female, ventrolateral view; d, antennular peduncle of female, ventral view.

strong conical tooth medially, and series of small serrate teeth (Fig. 3a).

Maxillule with slender bilobed endopodite; upper lacinia broad, distal margin with about 25 distal spines; lower lacinia with few long distal setae (Fig. 3b).

Maxilla with setose distal endite distinctly cleft, proximal endite setose with single lobe; palp short, thumblike, scaphognathite well developed (Fig. 3c).

Maxillipeds each provided with well developed exopod. First maxilliped with 2 endites separated by distinct notch. Palp distinctly segmented, provided near the base with accessory lobe. Epipod slender, distinctly bilobed (Fig. 3d).

Second maxilliped with 5-segmented endopodite. Dactylus short, as long as broad, with dense fringe of setae along dorsodistal margin. Propodus slightly shorter than carpus, also bearing numerous long simple setae (Fig. 3e).

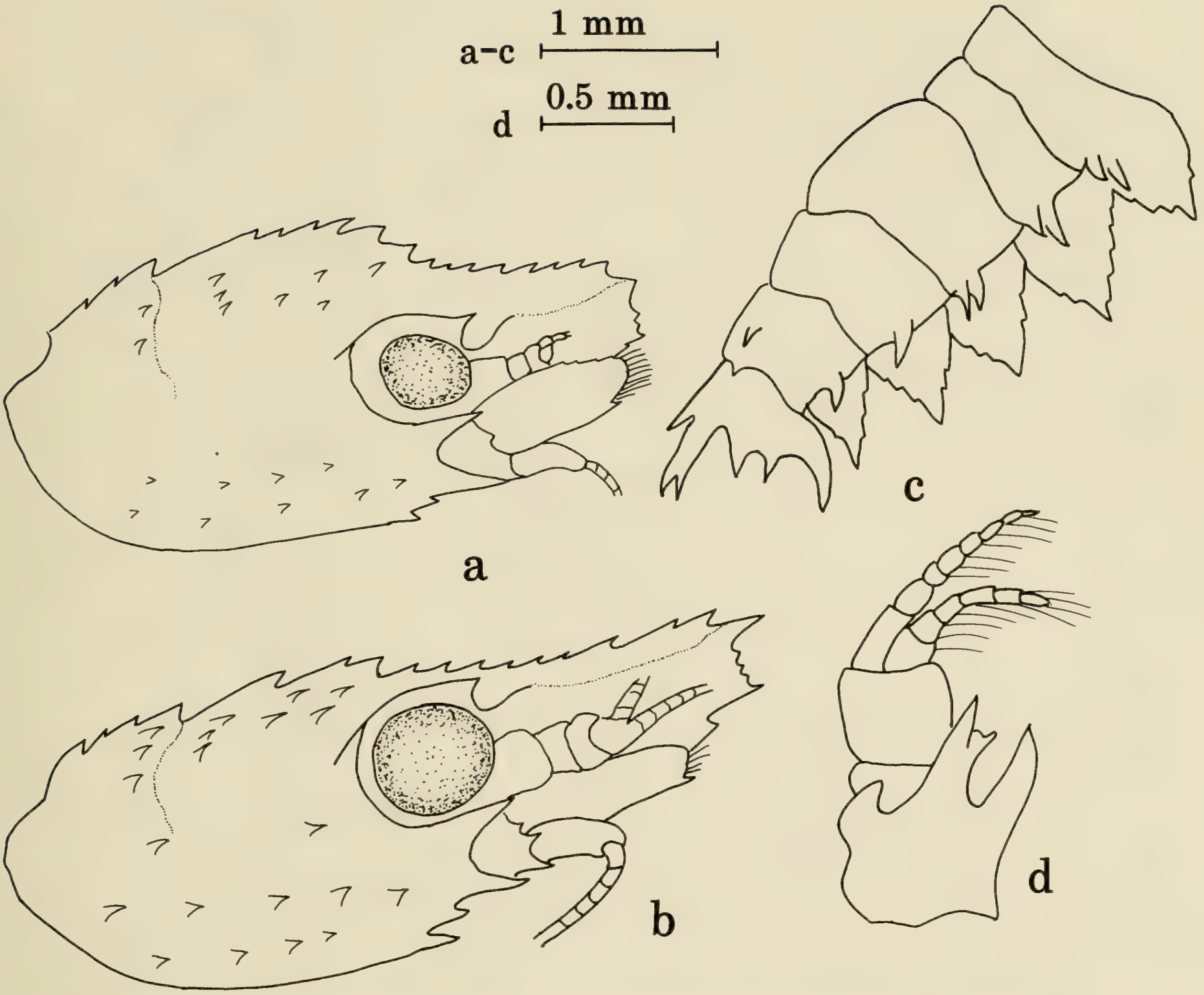

Fig. 2. *Trachycaris rugosa* Bate, males from South Carolina (USNM 224966) and Colombia (USNM 252485). a, carapace of juvenile; b, carapace of adult; c, abdomen of adult, ventrolateral view; d, antennular peduncle of adult, ventral view.

Third maxilliped robust, exceeding antennular peduncle by tip of ultimate segment, endopodite well developed, 4-segmented. Ultimate segment about twice as long as penultimate segment, bearing 7 strong dark spines. Penultimate segment slightly shorter than antepenultimate; on dorsal surface bearing 3 rows of terminal spines variable in number (first row 6–8, second 8–10, third 10–18). Antepenultimate segment bearing large spine on outer anterolateral angle and 2 rows of setae on dorsal surface (first row 2–10, second 6–8). Exopod long, slender, reaching anterolateral spine of antepenultimate segment (Fig. 3f).

First pereiopods small, rather heavy, reaching middle of merus of third maxillipeds. Finger acute, about ⅗ as long as palm, fixed finger ending in 2 black claws. Palm somewhat swollen, produced posterior to articulation with carpus. Carpus short, slightly longer than broad, about ⅔ the length of the chela. Merus and ischium slightly longer than carpus (Fig. 4a).

Second pereiopods equal and slender. Finger nearly ⅓ as long as palm. Carpus about 1.5 times as long as chela, consisting of 2 joints of equal length. Merus slightly longer than chela (Fig. 4b).

Last 3 legs robust, short. Third pereiopod exceeding antennal peduncle by entire length of carpus. Posterior margin of dactylus with 3–5 teeth, distal one largest; propodus nearly twice as long as dactylus, posterior margin

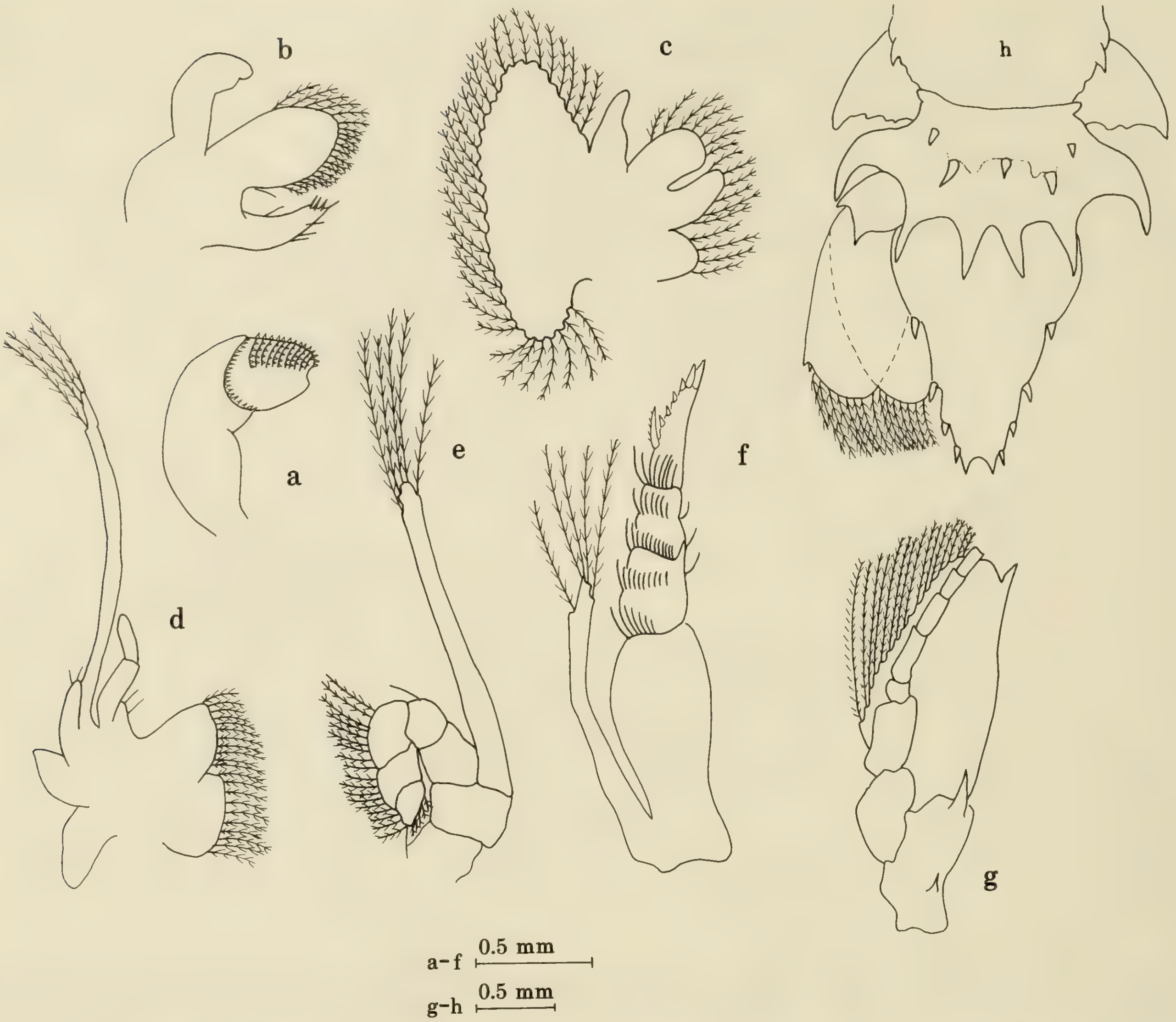

Fig. 3. *Trachycaris rugosa* Bate, male from Colombia (USNM 252485). a–f, mouth parts, right external view: a, mandible; b, maxillula; c, maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped, dorsal view; g, antenna, ventral view; h, telson and sixth abdominal somite.

bearing 4 spinules; carpus about half length of merus, bearing 4 or 5 strong spines on dorsal surface, ventral margin with strong spine at anterior point (Fig. 4c, d); dorsal surface of merus with 2 spines on inner margin, and 2 spines near middle. Fourth and fifth pereiopods similar to third (Fig. 4e, f).

Abdomen having anterior 2 somites with lateral, short grooves, third to sixth somites smooth. Males with abdominal pleura large, narrow (Fig. 2c). Apexes of first to fifth pleura ending in marginal teeth with minute denticles (generally 2 or 3). First to third abdominal somites armed with 2 strong ventromedian abdominal spines, fourth and fifth somites bearing only 1 ventromedian spine. Females with pleura broadly rounded, also with minute denticles (generally 3 or 4). Juvenile females armed on first to third somite with 2 small ventromedian abdominal spines, fourth and fifth with a single spine. Immature females (LT ≤ 11.5 mm) still having 1 ventromedian spine on both fourth and fifth somite (Fig. 1c). Ovigerous females lacking all ventromedian abdominal spines. Fifth abdominal somite in females and males with large spine on lateral surface of pleura. Sixth somite with very narrow pleura ending in strong posterior spine without minute denticles and bearing

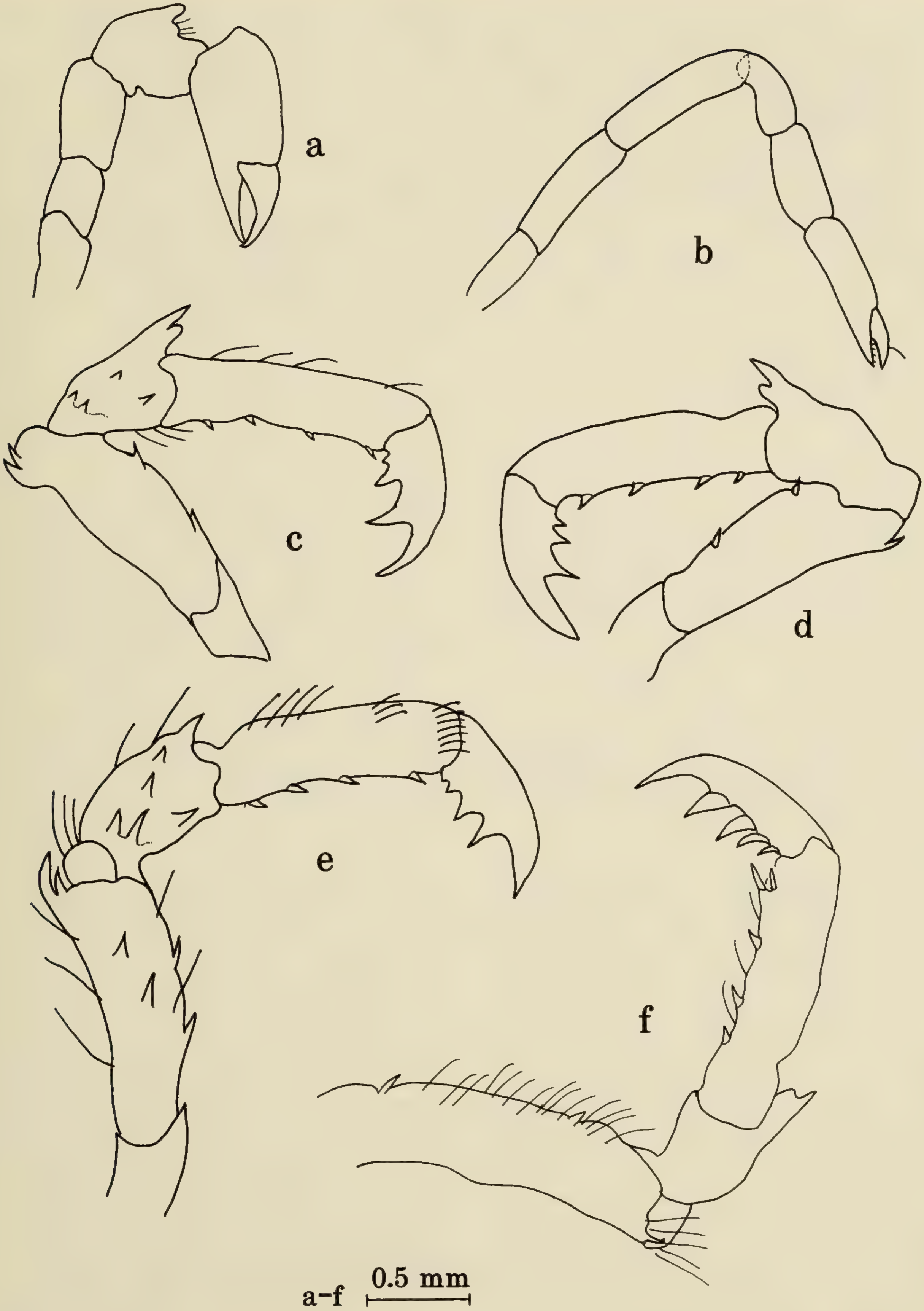

Fig. 4. *Trachycaris rugosa* Bate, male from Colombia (USNM 252485) and female from Puerto Rico (USNM 1135). a, first pereiopod of male; b, second pereiopod of male; c, third pereiopod of male, dorsal view; d, third pereiopod of male, ventral view; e, fourth pereiopod of female, dorsal view; f, fourth pereiopod of female, ventral view.

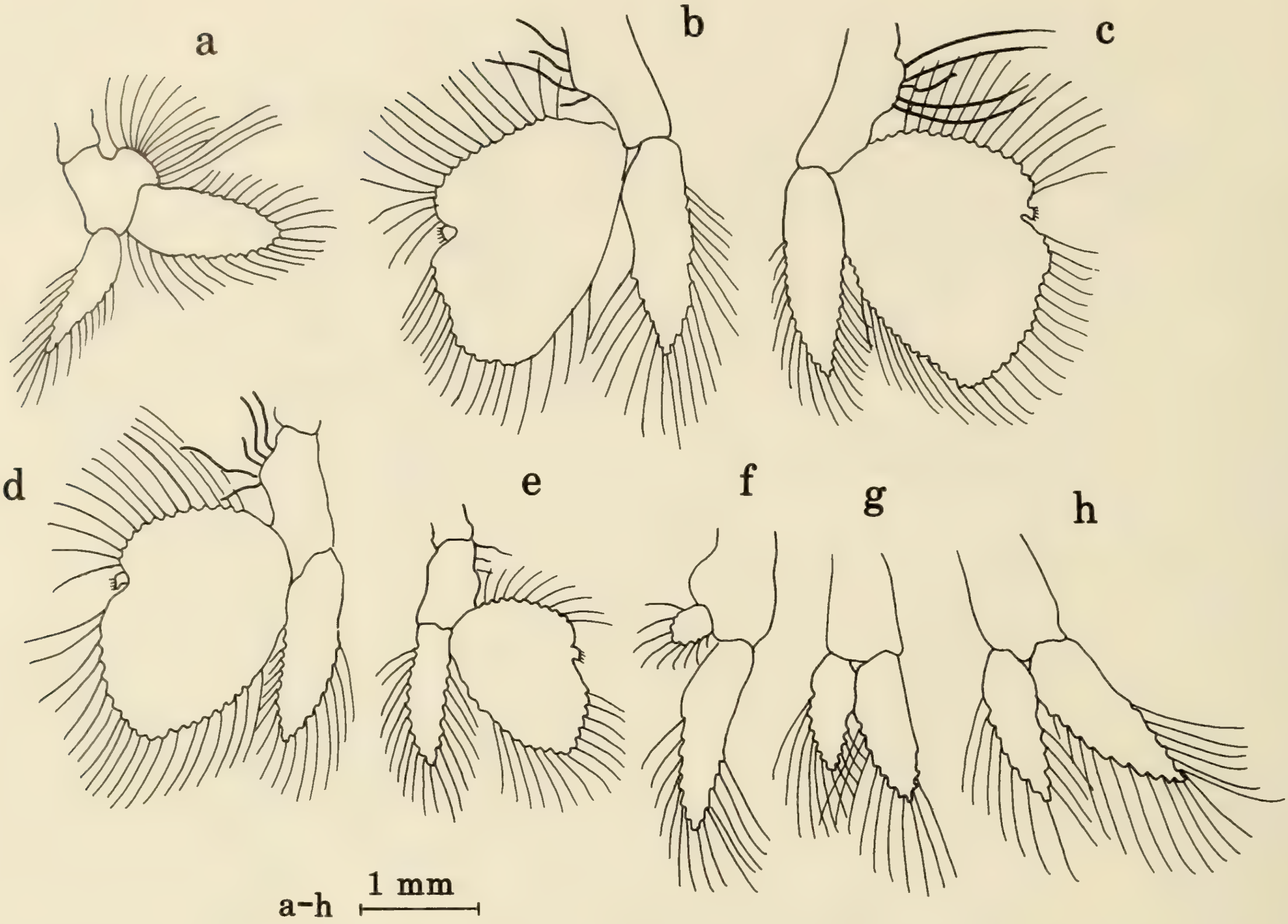

Fig. 5. *Trachycaris rugosa* Bate, female from Puerto Rico (USNM 1135) and male from Colombia (USNM 252485). a, first pleopod of female; b, second pleopod of female; c, third pleopod of female; d, fourth pleopod of female; e, fifth pleopod of female; f, first pleopod of male; g, second pleopod of male; h, third pleopod of male.

4 large, strong terminal spines similar in size; another 3 large spines are on dorsal surface alternately placed between 4 terminal spines (Fig. 3h).

Telson broadly oval, with blunt apex. Lateral margin each bearing 4 movable spines. Anterior pair of spines located anterior to middle of telson, second pair placed midway between first spine and posterior end of telson (Fig. 3h). Two posterior pairs smaller, similar in size near the apex.

Uropods well developed. Exopodite distinctly broad with outer margin slightly rounded and ending in tooth; inner side bearing movable spine often difficult to observe in juveniles. Endopodite narrowly ovate, fringed with plumose setae (Fig. 3h).

Pleopods biramous, first pleopods smallest in females, with narrow endopodite twice as long as basipodite and longer than endopodite. First pleopods lacking appendix interna (Fig. 5a). Second to fifth pleopods bearing a very small rounded appendix interne ending in tiny curved hairs. Second pleopods with broad discoidal endopod about 1.3 times longer than wide, exopodite narrow (Fig. 5b). Second to fifth pleopods generally similar, third pleopod largest, decreasing in size posteriorly (Fig. 5b–e). In males, first to fifth pleopods biramous, all lacking appendices. First pleopods with very small and rounded endopodite and large and narrow exopodite. Second to fifth pleopods similar in shape and size (Fig. 5f–g).

Measurements.—♀ ovig. TL = 11.12–29.3 mm, CL = 5.7–12.5 mm; ♀ non-breeding

LT = 5.4–11.12 mm, LC = 2.57–5.70 mm. ♂ LT = 6.96–11.32 mm, LC = 3.03–5.65 mm.

Color.—In life, abdomen and carapace bright red with some white spots in distal part of rostrum, orbit of eye, telson and outer edge of pleura. Pereiopods with transverse irregular white and red bands, except on the second pair. This color pattern appears to be mimicry, as the specimens were found living on calcareous algae of a similar red-pinkish color. Color of preserved material is variable, some specimens keeping a dark brown color, while in others the color disappears entirely.

Distribution.—Western Atlantic from South Carolina through Gulf of Mexico and Caribbean Sea to Santa Marta, Colombia.

Remarks.—The genus *Trachycaris* Calman (1906) was founded to receive *Platybema rugosus* Bate, 1888, a species that until 1940 was known only from the western Atlantic (Gurney 1940). Holthuis (1949) compared material of *T. rugosa* from the Canary Islands and a single *T. rugosa* specimen from Curaçao with material of *T. restricta* A. Milne Edwards from the Cape Verde Islands, and concluded that the eastern and western Atlantic forms should be one species, *T. restricta.* The Curaçao and Canary Island specimens differed in several significant details from Bate's figures, leading Holthuis to conclude that Bate's drawings of the western Atlantic specimen were inaccurate, and that both forms should be considered as one species. Although Holthuis accurately described and compared the specimens he observed, he may have wrongly assumed that Bate's descriptions of the mandible were inaccurate.

Noteworthy variations in morphology were found among the specimens of *T. restricta* in the USNM collection, due in part to sexual dimorphism and age. In addition, significant differences were found between the ovigerous females in the USNM collection and Holthuis's description of an ovigerous female of *T. restricta.* The main differences are: lack of a palp on the mandible; two spines on the basal antennal peduncle instead of three; two-segmented palp of the first maxilliped; lower endite of the maxilla present; ventral surface of the antennular peduncle with a large curved spine; and several rows of spines on the third maxilliped.

These characteristics were shared by all but one of the 19 females in the USNM collection. The sole exception, a female from Bermuda, showed the mandible, the antennal peduncle, and the first maxilliped as in Holthuis's (1949) description of *T. restricta.* The other differences between Holthuis's description and the characteristics observed in the USNM material may be due to inaccuracies in the description, because these structures appear different when viewed from ventral and dorsal perspectives. Until it is possible to compare greater number of specimens from the eastern and western Atlantic to determine the extent of variation of this species, it is best to separate the east Atlantic species, *T. restricta,* from the west Atlantic species, *T. rugosa.*

Kemp (1914) described variation in the proportional lengths of the third maxillipeds and first pereiopods of males of the hippolytids *Saron marmoratus* and *Alope australis* from young adulthood to senility. In addition, females and males of *Latreutes mucronatus* exhibited a remarkable diversity in the form of the rostrum as well as the proportions of the antennal scale and the spinulation of the anterolateral margin of the carapace. Sexual dimorphism in other hippolytids has been reported in *Lebbeus polaris, Spirontocaris liljeborgii* and *S. phippsii,* with differences found mainly in the shape and length of the rostrum, which become more pronounced with increasing age (Greve 1963, Squires 1965). Chace (1972) reported a large difference in size between males and females of *Thor dobkini.* Although some hippolytids, like *Spirontocaris* spp., possess ventral abdominal spines

(Greve 1963), they are not considered to be an indication of sexual dimorphism. Sexual dimorphism in the hippolytid *Trachycaris rugosa* is based mainly on the presence of ventromedian abdominal spines in the males, lack of appendices in all the pleopods in the males, more rounded abdominal pleura in females, different proportion of segments in the antennular peduncle, and different spination and shape of the carapace. Similar features were reported by Goy & Felder (1988) in the stenopodid *Microprosthema manningi.*

Males of *T. rugosa* of the USNM collection, which are smaller and less abundant, come from only two different localities: South Carolina (U.S.A.) and Isla de Aguja (Colombia). The South Carolina specimens were collected by suction sampler between 33–68 m in depth, and the Colombian specimens were collected by hand in 25 m among calcareous algae. Females examined were collected in different parts of the Caribbean, Gulf of Mexico and Bermuda, in depths between 8–20 m, on sand or coral. Based on this information, it is reasonable to conclude that males are more cryptic and live in deeper water than females, and that these differences in habitats could possibly account for morphological differentiation.

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105(3), 1992, pp. 571–574

A NEW GENUS FOR *CORALLIANASSA XUTHA* MANNING (CRUSTACEA: DECAPODA: CALLIANASSIDAE)

Raymond B. Manning

Abstract.—The new genus *Corallichirus* is recognized for species formerly placed in *Corallianassa* that have subequal second and sixth abdominal somites. This new genus contains two American and at least one Indo-West Pacific species.

Among the genera recognized by Manning & Felder (1991) in their revision of American genera of callianassid ghost shrimps is *Corallianassa* Manning, 1987. This genus contains two groups of species that can be separated on the basis of the length of the second abdominal somite. In the group containing the type species, *Corallianassa longiventris* (Milne Edwards, 1870) from the western Atlantic, the second abdominal somite is much longer than the sixth (Fig. 1a), as long as the sixth somite and telson combined. In the second group, the second somite is no longer than the sixth (Fig. 1b); this group contains two American species, *C. hartmeyeri* (Schmitt, 1935) and *C. xutha* Manning, 1988.

A second difference, size of adults, also can be used to distinguish members of the two groups of species. A new genus is recognized here for the smaller species with the short second abdominal somite.

Abbreviations used below include: A1, antennule; A2, antenna; mm, millimeters; Mxp3, third maxilliped; Plp1–5, first to fifth pleopods. Total length is measured on the midline and carapace length is postorbital carapace length.

Family Callianassidae Dana, 1852
Subfamily Callichirinae Manning & Felder, 1991
Corallichirus, new genus
Figs. 1b, 2

Type species.—*Corallianassa xutha* Manning, 1988.

Definition.—Size small, adults not exceeding 60 mm in total length. Carapace with dorsal oval and rostral spine, lacking cardiac prominence and rostral carina; anterior margin of carapace with 3 spines, median extending to cornea. Cornea subglobular, appearing terminal. A1 peduncle not stouter than A2 peduncle. Mxp3 subpediform, without exopod; merus not projecting beyond articulation with carpus. Chelipeds unequal, major lacking meral hook. Second abdominal somite subequal in length to sixth somite. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both sexes; male Plp2 without appendix masculina; appendices internae present on Plp2–5 in both sexes: digitiform and distal on Plp2, articulated, extending as palp beyond margin of endopod on Plp3–5.

Included species.—Two from the Americas, *Corallichirus hartmeyeri* (Schmitt, 1935), new combination, from Jamaica and Ascension Island (Manning & Chace 1990), and *Corallichirus xuthus* (Manning, 1988), new combination, from localities between Baja California and the Galapagos Islands in the eastern Pacific.

Callichirus placidus (De Man, 1905), new combination, from the Indo-West Pacific, is also placed in this new genus, as it too has a short second abdominal somite.

Etymology.—The name is derived from the Greek, *korallion,* coral, and *cheir,* hand; it combines the generic names *Callichirus* and *Corallianassa.* The gender is masculine.

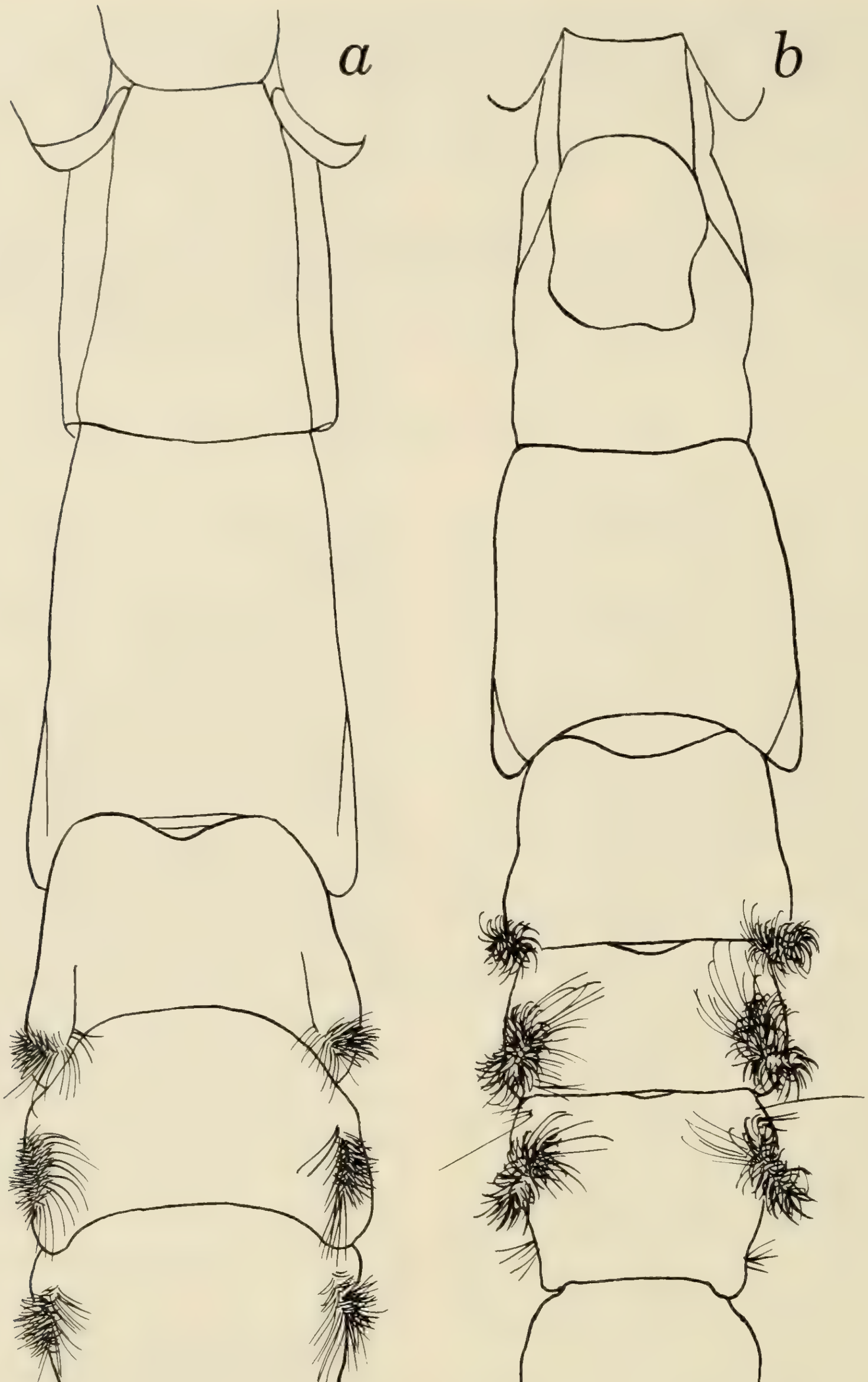

Fig. 1. Abdomen in dorsal view of: a, *Corallianassa borradailei* (De Man, 1928a) (from Manning 1987: fig. 9b); b, *Corallichirus xuthus* (Manning, 1988) (from Manning 1988: fig. 3g).

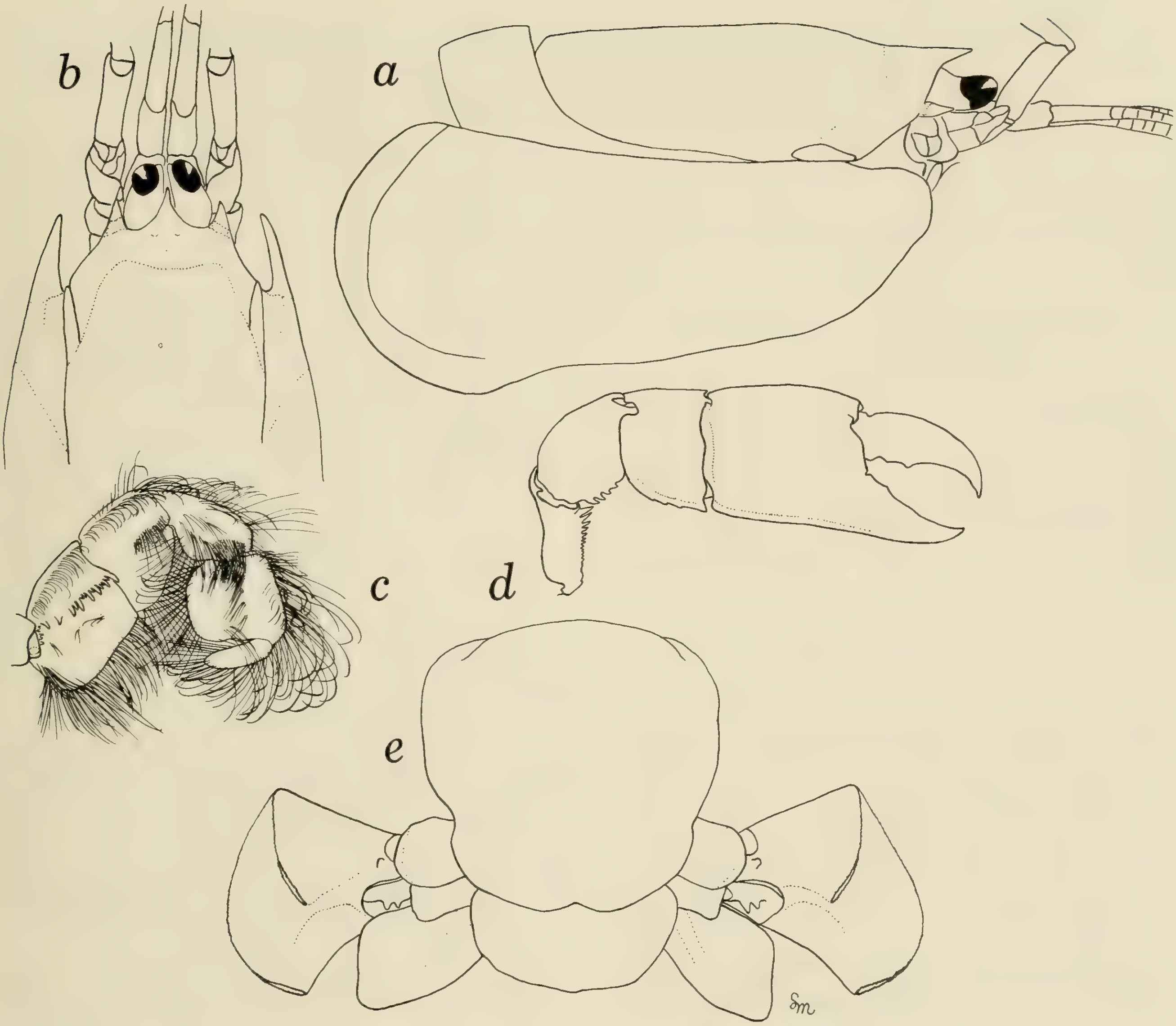

Fig. 2. *Corallichirus xuthus* (Manning, 1988). Ovigerous female, Clipperton Island, total length 55 mm. a, Carapace and frontal appendages, lateral view; b, Anterior part of carapace and anterior appendages, dorsal view; c, Mxp3, inner face; d, Major cheliped, outer face; e, Sixth abdominal somite and tail fan. (From Manning 1988: fig. 3a–d, i.)

Remarks.—*Corallichirus* is erected for species formerly placed in *Corallianassa* in which the second abdominal somite is subequal in length to the sixth abdominal somite (Fig. 1b). *Corallianassa* is restricted to species in which the second abdominal somite is distinctly longer than the sixth somite, almost as long as the sixth somite and telson combined (Fig. 1a). This diagnostic feature was used by De Man (1928b:108, 171) and subsequently by Manning (1988: 888) to differentiate species of *Corallianassa*.

Another feature that may help to distinguish members of these two genera is maximum size. Whereas adults of *Corallianassa longiventris* may attain a total length of 100 mm and a maximum carapace length of 25 mm (based on specimens from Lake Worth, Florida in collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.), members of *Corallichirus* are much smaller, with a maximum total length of 55 mm and a maximum carapace length of less than 10 mm (Manning 1988).

I consider the dissimilarity in length of the second abdominal somite in members of *Corallianassa* and *Corallichirus* to be a fundamental morphological difference. It certainly reflects a major difference in the amount of space required for an animal to turn in its burrow, thereby in part determining the shape of the burrow which must be very different in members of the two genera.

Acknowledgments

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DESCRIPTION OF THE MATURE FEMALE AND EPICARIDIUM LARVA OF *CABIROPS MONTEREYENSIS* SASSAMAN FROM SOUTHERN CALIFORNIA (CRUSTACEA: ISOPODA: CABIROPIDAE)

Clay Sassaman

Abstract.—The cryptoniscoid isopod *Cabirops montereyensis* Sassaman, previously known only from Monterey Bay, California, has been collected at Malibu, California. Diagnostic characters of the cryptoniscus larva are illustrated with scanning electron microscopy and the mature female and epicaridium larva are described. The mature female exhibits characteristics typical of most species in the genus, especially those parasitic on pseudionine bopyrids. The epicaridium larva differs from other described Cabiropidae in details of the appendages and in the possession of a prominent anal tube.

Cabirops Kossmann, 1884 is a genus of hyperparasitic isopod crustaceans that are brood parasites of bopyrid isopods which are, in turn, branchial parasites of decapod shrimps and crabs. *Cabirops* has a complex taxonomy stemming from confusion about the relationship between it and *Paracabirops* Caroli, 1953, which is now considered a junior synonym (Restivo 1975), and from the number of unnamed species which have been assigned to this genus. I have reviewed the nomenclature of the fifteen described species of *Cabirops* elsewhere (Sassaman 1985) and follow those conventions here; the superfamily nomenclature has been reviewed recently by Grygier & Bowman (1990, 1991).

Although the genus is widespread in its occurrence throughout the world, only one species, *Cabirops montereyensis,* has been described from the entire eastern Pacific Ocean. Its known distribution has been limited to Monterey Bay, California; previous collections of its definitive host, *Aporobopyrus muguensis,* parasitizing porcellanid crabs of the genus *Pachycheles* in central and southern California did not yield this species (Sassaman 1985).

I have found specimens of *Cabirops* in four *Macrocystis* holdfasts collected at Malibu, California, over the last three years. Comparisons of cryptoniscus larvae and immature females between these collections and those from Monterey Bay indicate that the southern California specimens represent a range extension of *C. montereyensis.* The diagnosis of the cryptoniscus stage is illustrated, and supplemented by descriptions of several new characters, based on scanning electron microscopy.

Neither the mature female nor the epicaridium stage of *C. montereyensis* has been described. The southern California collections include a mature female brooding epicaridium stage larvae; these stages are described and compared with similar stages in other species.

Superfamily Cryptoniscoidea
Kossmann, 1880
Family Cabiropidae Giard &
Bonnier, 1887
Cabirops Kossmann, 1884
Cabirops montereyensis Sassaman, 1985
Figs. 1A–I, 2, 3A–H, 4A–I

Materials examined.—Specimens from southern California were extracted from

Macrocystis holdfasts collected by Rimmon C. Fay (Pacific Bio-Marine Laboratories) at Malibu, California, at depths from 8 to 10 m as follows: 8 Jan 1988, 1 cryptoniscus larva from branchial cavity of *Pachycheles holosericus* parasitized by an unpaired female *Aporobopyrus muguensis*; 22 May 1989, 1 cryptoniscus larva found free in residue from holdfast; 2 May 1990, 1 cryptoniscus larva and 1 immature female in marsupium of 1 unpaired *A. muguensis* and 2 cryptoniscus larvae and 2 females (1 immature and 1 mature) in marsupium of second (paired) *A. muguensis,* each bopyrid in branchial cavity of *P. holosericus,* 11 additional *A. muguensis* unparasitized; 4 February 1991, 9 cryptoniscus larvae on 1 paired *A. muguensis* in branchial cavity of *P. holosericus,* 6 additional *A. muguensis* unparasitized.

All material was fixed in 70% ethanol except the cryptoniscus collected in May 1989 and six cryptoniscus larvae collected in February 1991, which were fixed in 3% glutaraldehyde in sea water. The May 1989 specimen was subsequently prepared for scanning electron microscopy (SEM) with the protocol of Nielsen & Strömberg (1973a), gold-palladium coated, and examined with a Philips 515 microscope. Epicaridium larvae were dissected from the marsupium of the mature female and prepared for SEM by the same procedure.

The 3 females collected on 2 May 1990, their accompanying males, bopyrid hosts, and decapod hosts have been deposited with the Los Angeles County Museum of Natural History under catalog number LACM 90-90.

Cryptoniscus larva.—Comparison of the cryptoniscus larvae from Malibu with material from Monterey Bay indicates that the southern California specimens are *Cabirops montereyensis.* Diagnostic characteristics of *C. montereyensis* that are also present in the new material include the configuration of the lateral dentition of the 2nd article of the 1st antenna (Fig. 1A), the shapes and distributions of the coxal plate denticles (Fig. 1B), the setal comb on the dactyl of peraeopod III (Fig. 1C), the bifid dactyls of peraeopods VI (Fig. 1D) and VII, and the branched setae at the base of the uropodal endopod (Fig. 1E). The fused mouthparts of the oral cone are shown in Figure 1F. I previously characterized the medial setae arising from the pleopodal sympods as simple; they actually terminate in a trifid process, the middle tine being barbed (Fig. 1G) as illustrated by Goudeau (1970) for *Hemioniscus balani* and Nielsen & Strömberg (1973b) for *Parapodascon stebbingi.*

To the previous description of this stage (Sassaman 1985) I add that the dorsal cuticle of the head has scattered circular depressions containing a single, central, short cilium (Fig. 1H) reminiscent of structures mentioned by Nielsen & Strömberg (1973a) and recently described by Bocquet-Védrine (1985) in *Crinoniscus equitans.* In addition, the dorsal surface of the cephalon and the pre-antennal ventral surface contain rows of circular button-like structures (Fig. 1H, I) which are easily observed as dark circles under highly polarized bright light. Although initially identified as glandular secretions in *Cironiscus dahli* on the basis of azocarmine-positive histological staining (Nielsen & Strömberg 1965), these structures clearly have a morphological basis in *Cabirops montereyensis* (Fig. 1H, I) and are evident in SEMs of several other cryptoniscoid species (Nielsen & Strömberg 1973b). Their function and their taxonomic usefulness have yet to be determined.

Mature female.—The 2 immature females collected 2 May 1990 correspond in morphology with the Stage A and Stage B females previously illustrated (Sassaman 1985). This similarity further supports the identification of the southern California specimens as *Cabirops montereyensis* which, in the immature female stages, differs from other described species of the genus (Sassaman 1985). Only the mature female (Fig. 2) is described here.

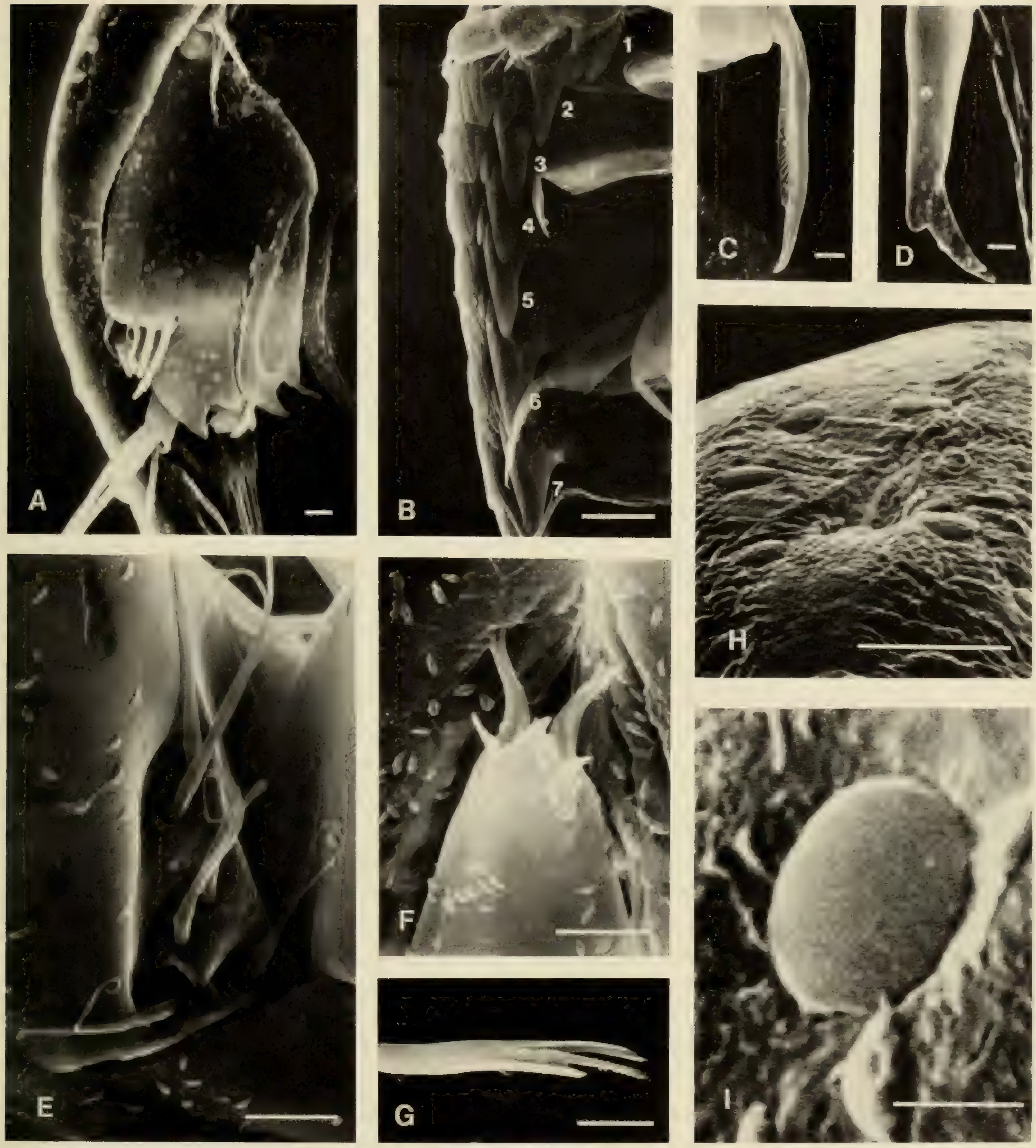

Fig. 1. *Cabirops montereyensis,* cryptoniscus larva. A, Second article of the first antenna; B, Coxal plates of peraeonal segments I–VII; C, Dactyl of peraeopod III; D, Distal tip of dactyl of peraeopod VI; E, Lateral margin of the uropodal endopod at its base; F, Oral cone; G, Distal tip of medial seta of pleopodal sympod 1; H, Sensory pit on dorsal surface of the cephalon at anterior margin; I, Detail of cephalic birefringent button. Scale bar in B = 50 μm; scale bars in A, C, E, F, G, and H = 5 μm; scale bars in D and I = 1 μm.

Description: Body strongly flexed ventrally into U-shape. Maximum dimension in flexed state 1.8 mm; total length (if unflexed) approximately 2.8 mm. Entire body filled with hatched epicaridium larvae. Cephalon indicated by paired cephalic plates and cup-shaped cephalic appendages projecting forward. Peraeon indicated dorsally by 7 regions each delimited by chitinous transverse ribs and cuticular creases. Perae-

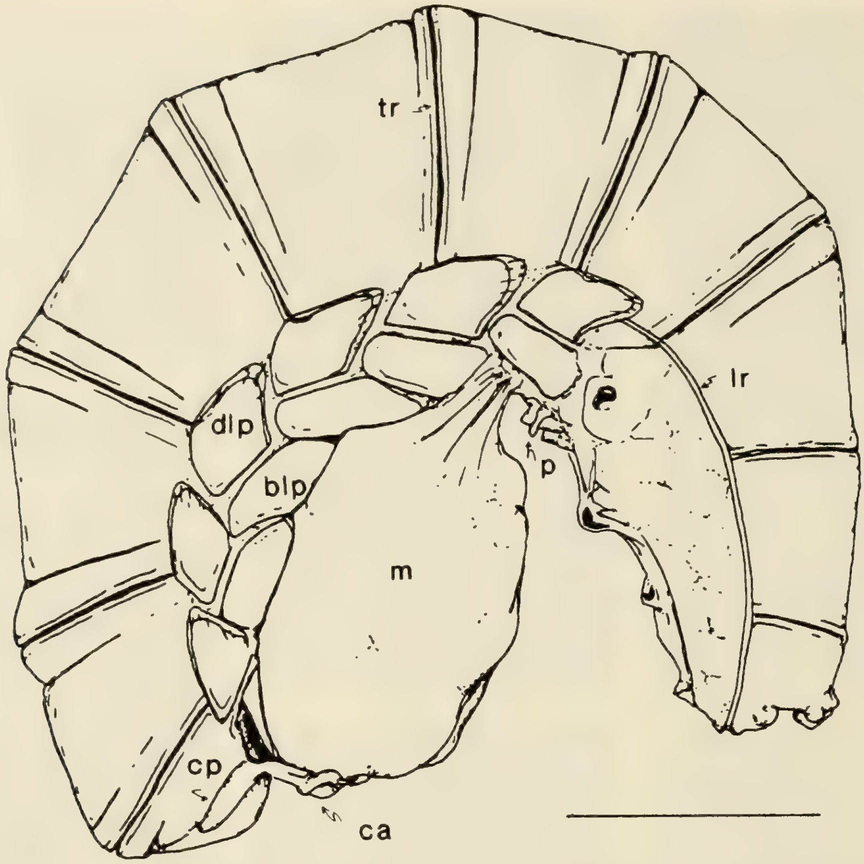

Fig. 2. *Cabirops montereyensis,* mature female. cp, cephalic plate; ca, cephalic appendage; blp, basal lateral plate; dlp, distal lateral plate; tr, transverse rib; lr, longitudinal rib; m, marsupium; p, papilla. Scale bar = 0.5 mm.

onal segments also indicated by 6 lateral-plate complexes composed of 2 elements, basal plate attached laterally and distal plate projecting postero-dorsally and partially free. Two large, laterally expanded, ventral lobes (marsupium) attached to peraeonal region. Small papilla extending ventrally on each side from last peraeonal segment. Pleon with 3 regions demarcated by transverse chitinous ribs, dorsal and ventral pleonal regions separated by prominent longitudinal chitinous rib. Ventral border with several irregular swellings. Pleon approximately 1:3 total body length.

Remarks: Adult females have been described previously for eight other species of *Cabirops*: *C. perezei* (Carayon 1942a), *C. marsupialis* (Caroli 1953, Reverberi & Catalano 1963, Restivo 1975), *Cabirops* sp. (Romano 1953, Attardo 1955), *C. codreanui* (Bourdon 1966), *C. ibizae* (Bourdon 1966), *C. pseudione* (Lemos de Castro 1970), *C. lobiformis* (Lemos de Castro 1970), and *C. reverberii* (Restivo 1971). Five features that are common to *C. montereyensis* and all but two of these species are: the body is ventrally flexed and has a characteristic U-shape in lateral view; laterally paired ventral swellings of the peraeonal region form a marsupium; six lateral plate-like processes are associated with the peraeon; traces of peraeonal segmentation are marked by transverse chitinous ribbing; and transverse segmentation of the pleonal region is indicated by dorsal and ventral regions separated by longitudinal ribbing.

One species, *C. perezei,* lacks obvious lateral plates and a marsupium. It is possible that the most advanced female described by Carayon (1942a), although brooding eggs, is not fully mature and therefore does not completely express the adult characters; the female he described subsequently (Carayon 1942b) is clearly not fully mature. Alternatively, *C. perezei* may represent a somewhat derived form; it is, for example, the only *Cabirops* in which eyes are lacking in the cryptoniscus stage. The second exception to the general pattern of adult female characters is *C. lobiformis,* which shows none of the typical characteristics of mature female *Cabirops.* Females of two additional species have been described: *C. lernaeodiscoides* (Kossmann 1872) lacks the marsupium and *C. tuberculatus* (Shiino 1942) resembles *C. lobiformis* in lacking most of the typical characteristics of mature females. Both of these descriptions probably are of immature females.

I have suggested, based on cryptoniscus morphology, that *Cabirops* may include two groupings of species, one associated with pseudionine and orbionine hosts and the other associated with bopyrine and ionine hosts (Sassaman 1985). Mature females of all species known from pseudionine hosts have been described and only *C. perezei* deviates from the general pattern of characteristics enumerated above. In contrast, adult females of species parasitic on ionine and bopyrine hosts are less well known, but it is within this group that the most notable exceptions in female morphology occur, e.g., *C. lobiformis* and perhaps *C. tuberculatus.* Further descriptions of *Cabirops* from these latter two host subfamilies are much needed to clarify this hypothesis of intrageneric heterogeneity. The *Cabirops* sp. parasitic on *Bopyrina ocellata* is a case in point. This species has been confused with *C. marsupialis,* a parasite of *Gyge branchialis,* and mature females have been differently described by Romano (1953) and Attardo (1955). Although Romano's illustration of the mature female (reproduced also by Attardo [1955]) does not show the chitinous ribbing and lateral plates, they are nevertheless evident in Attardo's (1955, fig. 11) photograph of the spent female. Clarification of the status of these bopyrine parasites may also have bearing on the affinities of *Cabirops* to *Bourdonia* Rybakov, 1990, a *Cabirops*-like genus recently described from *Bopyroides hippolytes.*

Among those species parasitic on pseudionine bopyrids, and showing the typical suite of *Cabirops* characters, there is, nevertheless, subtle variation in morphological features. Not all descriptions have indicated the presence of cephalic plates and cephalic appendages, and the relative size and the degree of segmentation of the pleon varies considerably (e.g., Bourdon 1966; Restivo 1971, 1975). The small papilla on the ventral surface of the peraeon of *C. montereyensis* appears to be unique.

Epicaridium larva.—General body form: in dorsal aspect of slightly flattened specimens, body drop shaped, widest at peraeonal segment V. Length measured from anterior edge of cephalon to posterior border of telson about 200 μm. Second antennae (excluding terminal spines) extending to pleonal segment 1.

Cephalon: Broadly rounded, dorsal cuticle smooth. No trace of eyes. Antenna 1 with 3 articles (Fig. 3A). Basal article incompletely resolved, but bearing at least 1 branched seta at antero-lateral corner. Second article simple, with 3 branched setae at distal edge. Third article biramous, dorsal branch simple with 2 terminal spines, ventral branch with 1 articulation, distal part bearing 3 terminal spines. Two aesthetascs originate at base of 3rd article. Antenna 2 of 5 articles (Fig. 3B): 2 peduncular, 3 flagellar. Distal peduncular article (Fig. 4B) with 4 setae: 3 dorsomedial (2 branched), 1 terminal. Two stout spines at distal ends of first 2 flagellar articles. Distal flagellar article with 4 short, smooth, terminal spines, and 2 longer ones with regular rows of short spinules along most of distal part, spinules more developed on shorter (outermost) of these spines (Fig. 4C) than on inner one (Fig. 4D). Mandibles terminating in row of bicuspid teeth forming grinding surface flanked laterally by cylindrical processes bearing terminal pores (Fig. 4E).

Peraeon: 6 segments with appendages.

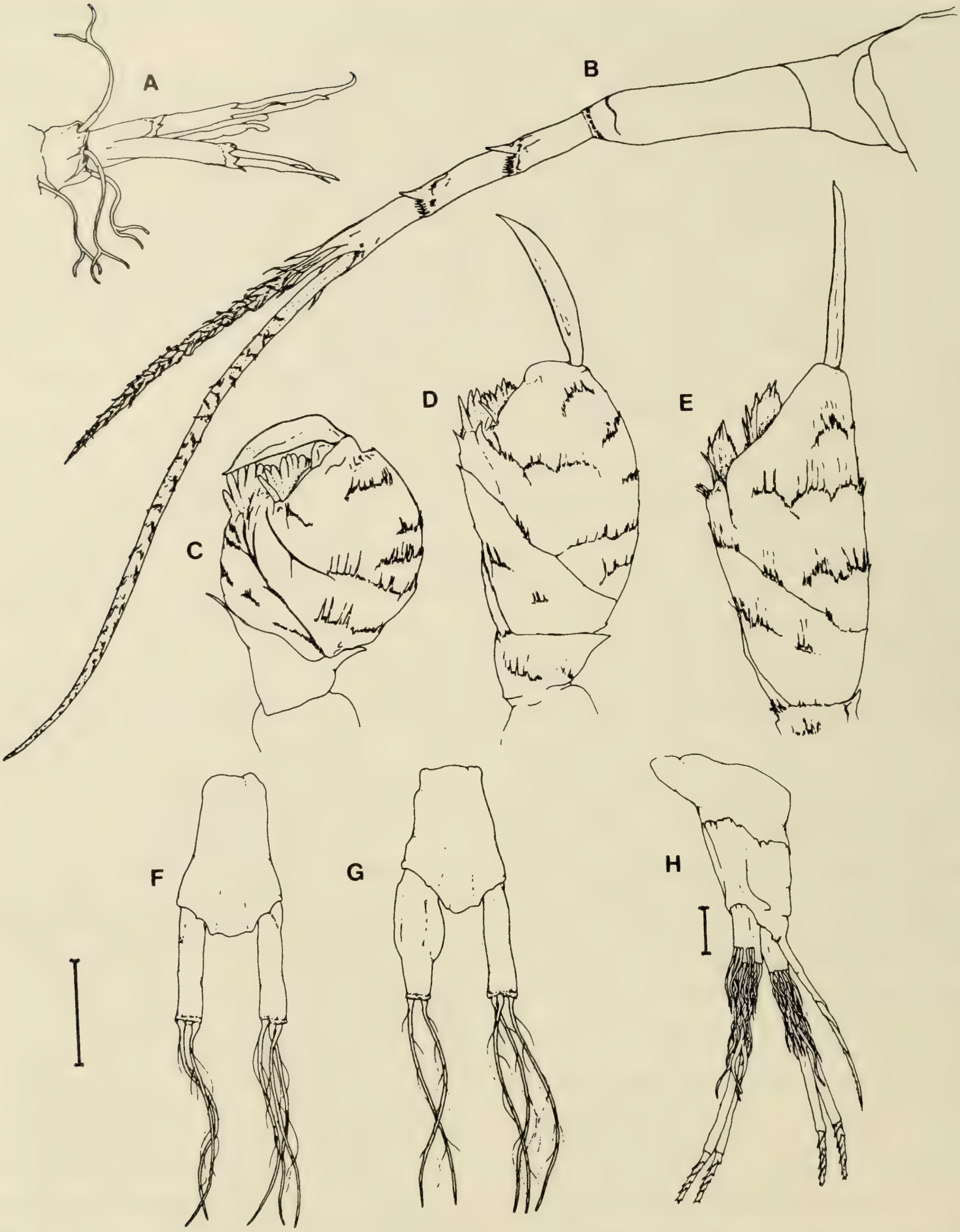

Fig. 3. *Cabirops montereyensis,* epicaridium larva. A, Antenna 1; B, Antenna 2, ventral view; C, Peraeopod I; D, Peraeopod V; E, Peraeopod VI; F, Pleopod 1; G, Pleopod 5; H, Uropod. Scale bars = 10 μm. (A–G are to the scale shown at the lower left of the figure.)

Each peraeopod with 6 articles, but carpus broadly fused to propodus on all peraeopods forming propodocarpal complex. Peraeopods I and II with bulbous propodocarpal complex (Fig. 3C), peraeopods III–V with more elongate complex, ending almost squarely (Fig. 3D), peraeopod VI with longest complex, tapering distally (Fig. 3E).

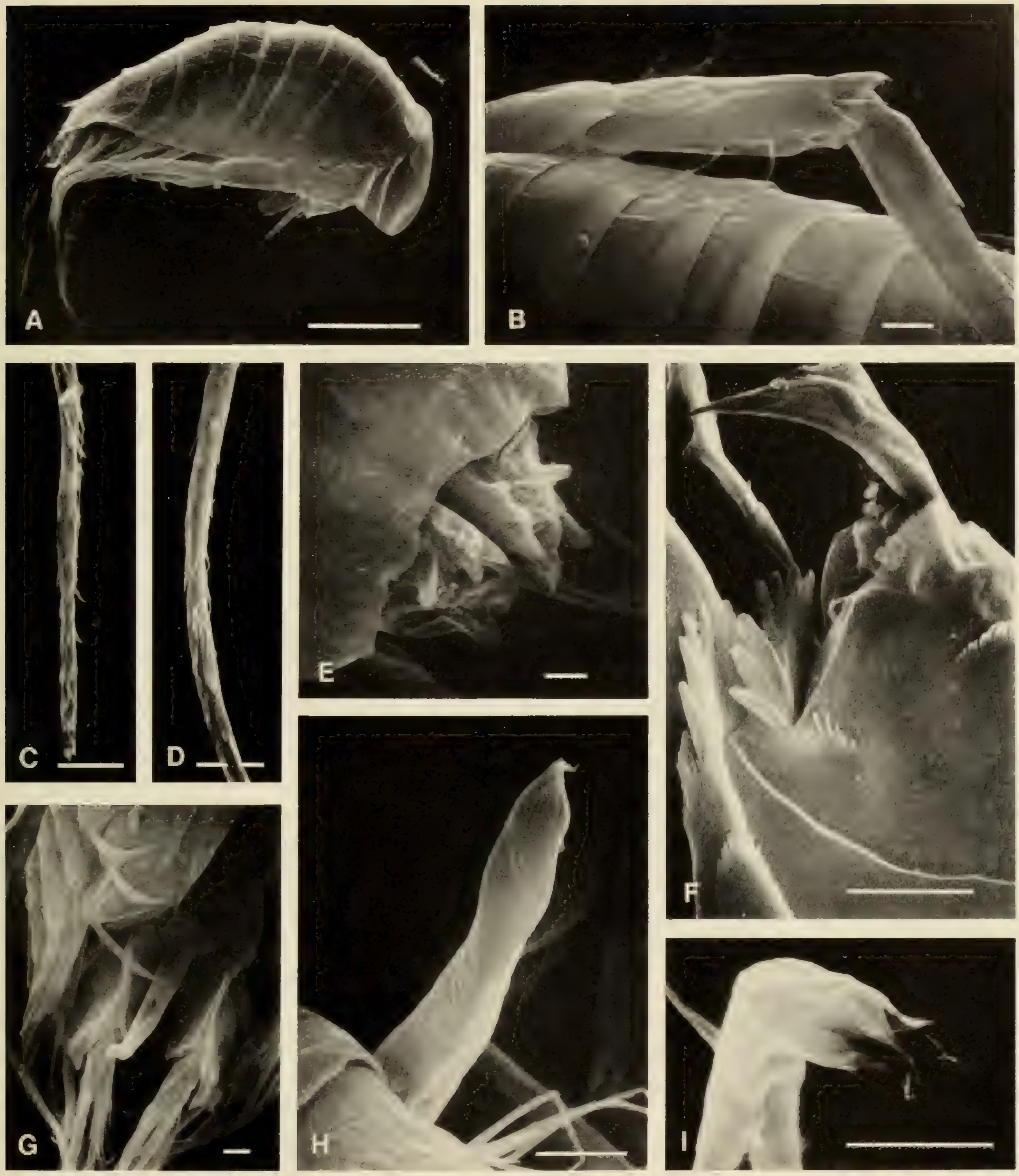

Fig. 4. *Cabirops montereyensis,* epicaridium larva. A, Lateral view, intact larva; B, Dorsal view of the distal penduncular article of Antenna 2; C, Outer terminal spine of antenna 2; D, Inner terminal spine of antenna 2; E, Mandibles; F, Distal tip of peraeopod V; G, Pleon with insertion of anal tube; H, Anal tube; I, Detail of terminal hairs of anal tube. Scale bar in A = 50 μm; scale bars in B, C, D, F, G, H, and I = 5 μm; scale bar in E = 1 μm.

Dentate shields on propodus and on distal tip of carpus on all peraeopods (Fig. 4F). Basis elongate on peraeopod VI.

Pleon: 5 pairs of biramous pleopods. Sympods lacking medial processes and progressively decreasing in length from pleopod 1 (Fig. 3F) to pleopod 5 (Fig. 3G). Exopods and endopods of similar length on all pleopods. All exopods with 3 terminal spines and all endopods with 2 terminal spines bearing fine setae. Uropods (Figs. 3H, 4G) robust. Protopod bearing lateral plumose spine, exopod with 3 spines (2 plumose) and endopod with 5 spines (2 plumose). Medial margins of uropodal endopod and exopod with fine hairs (Figs. 3H, 4H). Prominent anal tube originating at base of uropods (Fig. 4G), often projecting ventrally or anteriorly (Fig. 4H), terminal opening ringed with fine hairs (Fig. 4I).

Remarks: Previous descriptions of *Cabirops* epicaridium larvae (Romano 1953, Attardo 1955, Reverberi & Catalano 1963) are too fragmentary and imprecise to permit valid comparison with the larvae of *C. montereyensis.* Larvae of two other genera of Cabiropidae have been described in sufficient detail to permit general comparison: *Ancyroniscus bonnieri* (Holdich 1975) and *Clypeoniscus meinerti* (Giard & Bonnier 1895). These species differ from *C. montereyensis* in details of antennal, peraeopodal, and pleonal structures and both are characterized by very short anal processes. Similar generic level differences occur in the degrees of development of the anal tube within the Cryptoniscidae; it is prominent in *Liriopsis* (Caullery 1908), *Crinoniscus* (Pérez 1900, Boquet-Védrine 1987), and the enigmatic *Enthylacus* (Pérez 1920), but is lacking in *Danalia* (Caullery 1908, Fize 1955). The anal tube is well developed in *Hemioniscus balani,* the single species of Hemioniscidae in which the epicaridium stage has been described (Caullery & Mesnil 1901).

The only cryptoniscoid epicaridium that has been described in sufficient detail for precise comparison with *C. montereyensis* is *Crinoniscus equitans,* illustrated extensively by Bocquet-Védrine (1987). The two species are remarkably similar in the overall shapes of appendages and in the distribution and form of various spines and setae. Although there are differences in details of the second antennae, peraeopods, and pleopods, these differences are rather subtle. The salient difference between the two species is in the configuration of the uropods, slender and elongate in *C. equitans* and robust in *C. montereyensis.*

Uropodal morphology of epicaridia likely represents a familial character distinguishing Cryptoniscidae (Bocquet-Védrine 1987) from other families of Cryptoniscoidea. To what extent other differences in epicaridium morphology might represent characters of systematic value presently is unknown. This stage may be useful in future work in providing an additional suite of specific characters (as has been indicated for the bopyrid genus *Probopyrus*—Dale & Anderson 1982) and also, perhaps, in providing higher level characters which may aid in more firmly resolving the systematics of this superfamily.

Acknowledgments

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A NEW SPECIES OF *CORALLIODRILUS* (OLIGOCHAETA: TUBIFICIDAE) FROM THE EASTERN GULF OF MEXICO, AND A NEW RECORD OF *C. CORPULENTUS* FROM SOUTH CAROLINA

Christer Erséus and Michael R. Milligan

Abstract.—*Coralliodrilus priscus,* is described from off Tampa Bay, Florida. It is closely related to *C. corpulentus* Erséus, 1986, which is recorded here from off Charleston, South Carolina, but it differs from that species by its lack of modified posterior dorsal setae and its greater number of penial setae (about 20–25 as opposed to about 10–12 per bundle).

Coralliodrilus Erséus, 1979 (subfamily Phallodrilinae) is a marine genus of largely tropical and subtropical Tubificidae, and it currently contains fifteen species (Erséus 1990, 1992). One of these is *C. corpulentus* Erséus, 1986, previously known only from Hutchinson Island, east coast of Florida (Erséus 1986). Specimens of *C. corpulentus,* and material of a new, closely related species, were found by the second author while identifying benthic macroinvertebrates from two different dredge spoil disposal sites, in South Carolina and eastern Florida, respectively. Both taxa are reported in the present paper.

The worms were stained in paracarmine and mounted whole in Canada balsam prior to examination. The material is deposited in the United States National Museum of Natural History (USNM), Washington, D.C.

Coralliodrilus corpulentus Erséus, 1986
Fig. 1A

Coralliodrilus corpulentus Erséus, 1986:305–307, fig. 12.

New material.—USNM 148665-148666, 2 specimens from off Charleston, South Carolina, 32°38′32″N, 79°43′00″W, 15 m, medium sand with 39% carbonates (20 July 1989; Mote Marine Lab study of a disposal site of dredge spoils, for South Carolina Wildlife and Fisheries).

Remarks.—*Coralliodrilus corpulentus* was previously known only from off Hutchinson Island, east coast of Florida (Erséus 1986). The two new specimens from South Carolina are 4.8 and 6.0 mm long, with 54 and 55 segments respectively, and conform well with the original description. The penial setae, about 10–12 per bundle, are 70–75 μm long. The atria are 140–150 μm long, 55–70 μm wide, i.e., they are somewhat smaller than those of the type specimens (210–290 μm long, 55–80 μm wide). The outer muscular layer of the atria, however, is up to 16 μm thick in the new worms (maximally 12 μm in original material).

Many posterior dorsal setae are modified in this species; the upper tooth is much reduced, or lacking completely, while the lower tooth is prolonged and sharply pointed. One bundle of such setae from the new material is shown in Fig. 1A. *Corpulentus priscus,* n. sp., which undoubtedly is very closely related to *C. corpulentus,* does not have these modified setae (see below).

Distribution and habitat.—South Carolina (new record) and east coast of Florida. Subtidal carbonate sediments, 10–15 m depth.

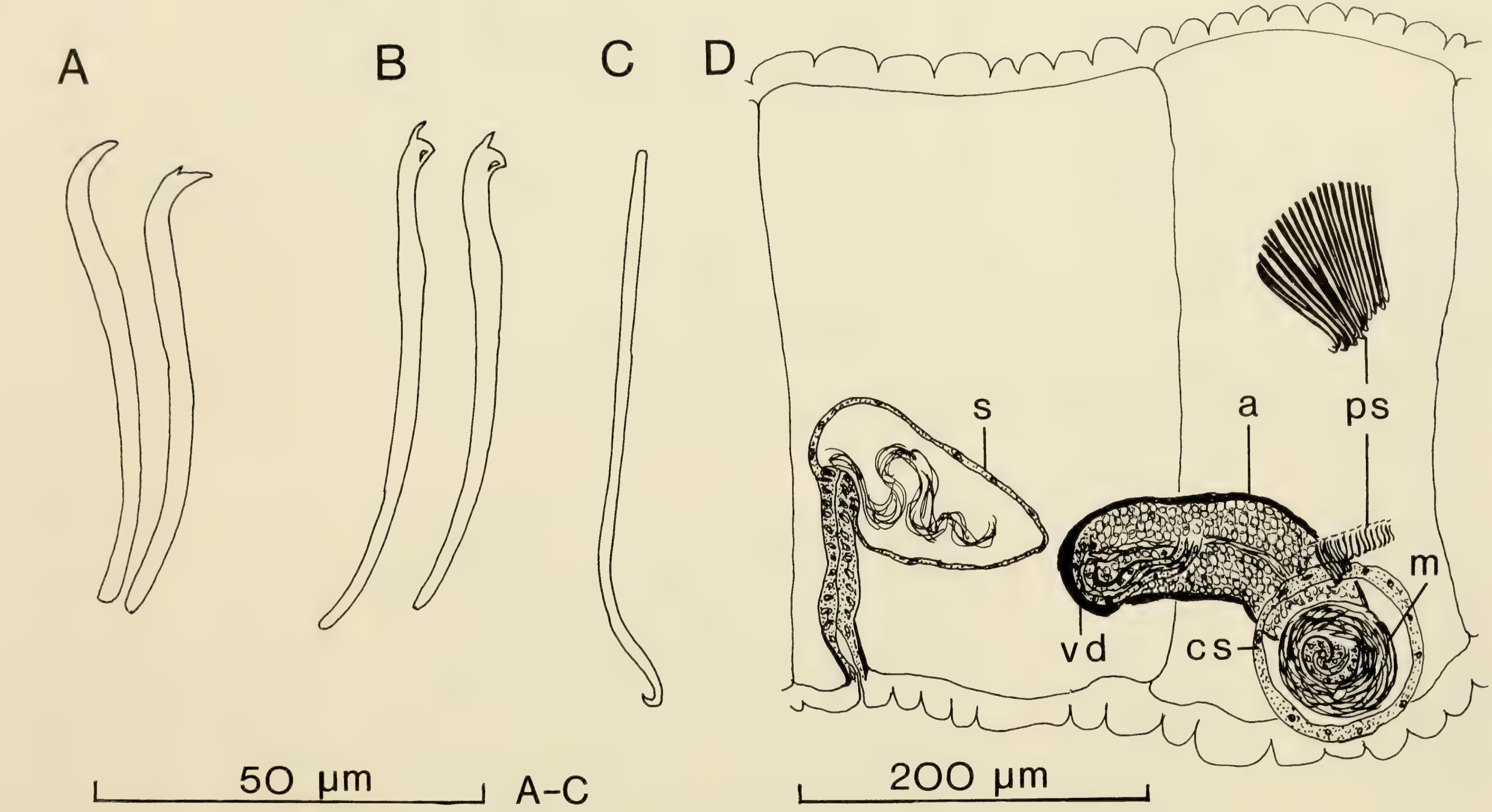

Fig. 1. A, *Coralliodrilus corpulentus.* Posterior dorsal somatic setae. B–D, *Coralliodrilus priscus.* B, Somatic setae; C, Penial seta; D, Lateral view of genitalia in segments X–XI. [Penial setae shown in full for one side of worm (upper right in Fig. 1D). For other side (the one with spermatheca and male depicted), only tips of penial setae indicated; these setae curved, much distorted, in specimen in question.] Abbreviations: a, atrium; cs, copulatory sac; m, muscular bulb; ps, penial setae; ss, spermatheca; vd, vas deferens.

Coralliodrilus priscus, new species

Fig. 1B–D

Holotype.—USNM 148668, whole-mounted specimen.

Type locality.—Gulf of Mexico off Tampa Bay, west coast of Florida, 27°32′48″N, 83°04′56″W, 24 m, medium sand with 15% silt and 3% organics (12 August 1987; Mote Marine Lab study of benthic communities in the vicinity of the Tampa Bay Material Ocean disposal site, for the United States Environment Protection Agency).

Paratype.—USNM 148667, 1 specimen from type locality; mounted on same slide as holotype.

Etymology.—Named *priscus* (Latin for 'old-fashioned'), as it lacks the advanced, modified dorsal setae in posterior segments, which characterize its closely related congener, *C. corpulentus.*

Description.—Length 6.2 and 7.0 mm, 55 and 52 segments, respectively. Width at XI, 0.42–0.44 mm. Prostomium rounded; short in holotype, elongate in paratype. Fixed specimens stout; segments short. Secondary annulation present, several annuli per segment. Clitellum poorly developed in both specimens. All somatic setae bifid (Fig. 1B), with upper tooth thinner and shorter than lower, and with subdental ligament. Bifids 40–70 μm long, 2–3.5 μm thick, (2)3(4) per bundle anteriorly, (1)2(3) per bundle in postclitellar segments. Penial setae (Fig. 1C, D; *ps*) slender and ectally hooked, 80–85 μm long, about 2 μm thick, at least about 20–25 per bundle (exact number difficult to establish). Male pores paired in line with ventral somatic setae, posteriorly in XI. Spermathecal pores paired in lateral lines, anteriorly in X.

Pharyngeal glands poorly developed, but appear to be present in at least V–VI. Male genitalia (Fig. 1D) paired. Vas deferens 12–14 μm wide, entering apical end of atrium; appears much shorter than atrium, but not observed in its full length. Atrium somewhat spindle-shaped, extending forward into X; main part of atrium (ampulla) 190–220 μm long, 60–70 μm wide, with ciliated and granulated inner epithelium, and muscular outer lining of varying thickness (2–12 μm). Ectally, atrium tapering into short (50–70 μm), narrow (18–20 μm) duct surrounded by very strong muscles. These muscles forming a compact, round bulb, about 60 μm wide, at middle of which atrial duct opens to exterior. Whole bulb appears enclosed in a round (shallow?) copulatory sac. Spermathecae (Fig. 1D, *s*) consisting of ducts, 70–100 μm long, 16–23 μm wide, and thin-walled, somewhat pear-shaped ampullae, 85–130 μm long, about 60 μm wide. Most ectal part of spermathecal ducts somewhat muscular. Spermathecal ampullae with coiled bundles of sperm.

Remarks.—This new species is very similar to *C. corpulentus,* also recorded in the present study, but it is easily distinguished from that taxon by its lack of modified somatic setae (cf. Fig. 1A), and its greater number of penial setae (about 20–25 as opposed to about 10–12 per bundle; see Erséus 1986). In addition, *C. priscus* appears to have somewhat less muscular atria than *C. corpulentus.* However, due to the great variation of this character in both species, even along the same atrium, it is diagnostically less useful.

Copulatory sacs, which are described for *C. priscus* here (Fig. 1D, *cs*), have not been observed in *C. corpulentus* (see Erséus 1986: fig. 12D).

Distribution and habitat.—Known only from the type locality, west coast of Florida. Subtidal medium sand, 24 m depth.

Acknowledgments

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PHYLLODOCIDS (ANNELIDA: POLYCHAETA) OF BELIZE, WITH THE DESCRIPTION OF THREE NEW SPECIES

Danny Eibye-Jacobsen

Abstract.—Phyllodocidae (polychaetes) from Belize are reported. Eight species are treated in detail. Of these, 3 are newly described: *Eumida muriatica, Sige belizensis,* and *Nereiphylla mimica. Pterocirrus foliosus* (Treadwell, 1924) is redescribed and the identities of *Hesionura elongata* (Southern, 1914), *Mystides borealis* Théel, 1879, and *Phyllodoce erythrophylla* (Schmarda, 1861) are discussed. Eight additional species are recognized, but not treated in detail due to the lack of sufficient material. Together with the previously recorded *Phyllodoce panamensis* Treadwell, 1917, 17 species are now known from Belize.

The presence of a Smithsonian field station on the island of Carrie Bow Cay in Belize has led to great improvements in our knowledge of the polychaete fauna of the western Caribbean Sea. Notable taxonomic contributions are by Fauchald (1980, Onuphidae), Fitzhugh (1983, Sabellidae), Young & Kritzler (1987, Terebellidae), Russell (1989a, 1989b, Syllidae), and Solis-Weiss & Fauchald (1989, Orbiniidae).

To date, the only published account of the Phyllodocidae of Belize is by Young & Young (1982), who reported the presence of three species: *Phyllodoce* (*Anaitides*) *panamensis* Treadwell, 1917, *Hesionura elongata* (Southern, 1914) and *Eulalia viridis* (Linnaeus, 1767).

During October and November of 1988 I visited Carrie Bow Cay. Several species of phyllodocids were collected, three of which were found to be new to science. This prompted the study of previously collected, undetermined phyllodocid material held at the National Museum of Natural History, Washington, D.C. (USNM). Sixteen species were found, eight of which are treated in detail below.

Materials and Methods

The 1988 collections were made near the following islands: Carrie Bow Cay, South Water Cay, Tobacco Cay, the Cocoas (east of northern end of Blue Ground Range), and the Sand Bores (east of the Cocoas). Earlier collected material had also been taken near Twin Cays and at Glover's Reef (for the locations of these islands see Rützler & Macintyre 1982). Details on all stations are given in the appendix. For the individual species below, material examined (for Belizean animals only) is indicated by the station numbers, in each case followed by the number of specimens from that station in parentheses. Data on non-Belizean material used for comparative purposes are given in the remarks section where appropriate.

Coral samples taken in 1988 each consisted of approximately 3.5 l of coral rubble with a drained weight of about 4.5 kg. Rubble was mechanically broken into smaller pieces and shaken in seawater to obtain live specimens. The pieces were then placed in a large bucket of seawater to which a few drops of clove oil were added. After about 12 hours, each sample was fixed in buffered 2% formalin. Individual pieces of coral rubble were subsequently washed in another bucket of seawater, where obvious specimens were removed with forceps, and the contents of both buckets then filtered through a 200 μm sieve. The material was once again fixed in 2% formalin and two days later was washed and transferred to 70% alcohol.

Sand samples were aerated from below causing specimens to rise into the water column, from which they were drained and sieved.

Specimens for SEM were critically point dried and sputter coated with platinum. Observations were made with a Cambridge Stereoscan 250 MK2.

All descriptions refer to animals from Belize. In the tentacular formulae used in description S = setae, 1 = tentacular cirrus, N = normal (ventral) cirrus, and 0 signifies the lack of either setae or cirrus. Types and other specimens are deposited in USNM and in the Zoological Museum of the University of Copenhagen, Denmark (ZMUC).

Family Phyllodocidae Ørsted, 1843

Genus *Hesionura* Hartmann-Schröder, 1958

Hesionura coineaui (Laubier, 1962)

Fig. 1

Mystides (*Pseudomystides*) *coineaui* Laubier, 1962:461, fig. 1a–g.

Eteonides coineaui.—Hartmann-Schröder 1963:222, figs. 30–32.

Hesionura elongata.—?Day 1973:19–20, fig. 3k–m.—Gardiner 1975:106, fig. 6b–d.—Young & Young 1982:119.—?Blake 1988: 248, fig. 2a–d.—Eibye-Jacobsen 1991: 532. [Not *Mystides* (*Mesomystides*) *elongata* Southern, 1914].

Hesionura sp. A Gathof, 1984:19-12, fig. 19-8a–c.

Material examined.—F-39 (3); F-41 (3); DEJ-1 (9, 1 used for SEM); DEJ-2 (1); DEJ-5 (8); DEJ-8 (1); DEJ-15 (3); DEJ-22 (14, 1 used for SEM).

Description.—Unless otherwise indicated based on largest specimen from st. DEJ-1. Length 12.5 mm (19 mm long in life), width excluding setae 0.5 mm, with 164 setigers (posteriorly incomplete).

Prostomium varying from semiglobular, slightly wider than long, to conical, longer than wide (Fig. 1A); 4 subulate antennae present, as long as prostomium in life; obvious eyes lacking; several specimens with 2 imbedded pigment spots of varying position and size on dorsoposterior area of prostomium; nuchal organs small, in dorsolateral depressions at posterior border of prostomium.

Proboscis densely covered with dark brown papillae arranged in 12 longitudinal rows (Fig. 1B); each papilla (diameter about 20 μm) crowned with claviform structures (diameter about 250 nm) apparently arranged in 2 concentric arcs (posterior on everted proboscis; observed using SEM); 7 oral papillae present, each about 50 μm in diameter, lacking micropapillae (only 1 specimen examined; st. DEJ-22).

Tentacular formula 1 + 0 1/1 + S 0/N; all tentacular segments fully developed, segment 1 weakly delineated from prostomium. Tentacular cirri of segment 1 subulate, reaching to segment 4 or 5; dorsal tentacular cirri of segment 2 subulate, reaching to segment 6; ventral tentacular cirri of segment 2 very short, cylindrical, not flattened as ventral cirri of following segments (viewed in SEM).

All dorsal cirri elongate oval, with drawn-out tip (Fig. 1C). Each neuropodium with 4 or 5 spinigerous compound setae; uppermost seta with distally trifid shaft (Fig. 1D); lowermost seta with distally bifid shaft (Fig. 1G); middle setae (2 or 3) with distally bifid shaft, each tooth with smaller, medial tooth (Fig. 1E–F); shafts of uppermost and lowermost setae notably thicker than those of middle setae, especially on posterior segments; distal articles of middle setae most elongate. All ventral cirri more elongate and larger than dorsal cirri, extending beyond neuropodial tips (Fig. 1C). Anal cirri very long and thin, about 15 times as long as width at base (Fig. 1H).

Living animals green, some very pale, with darker green spots (glands?) on dorsal and ventral cirri; green pigment becoming brown following preservation. Several specimens

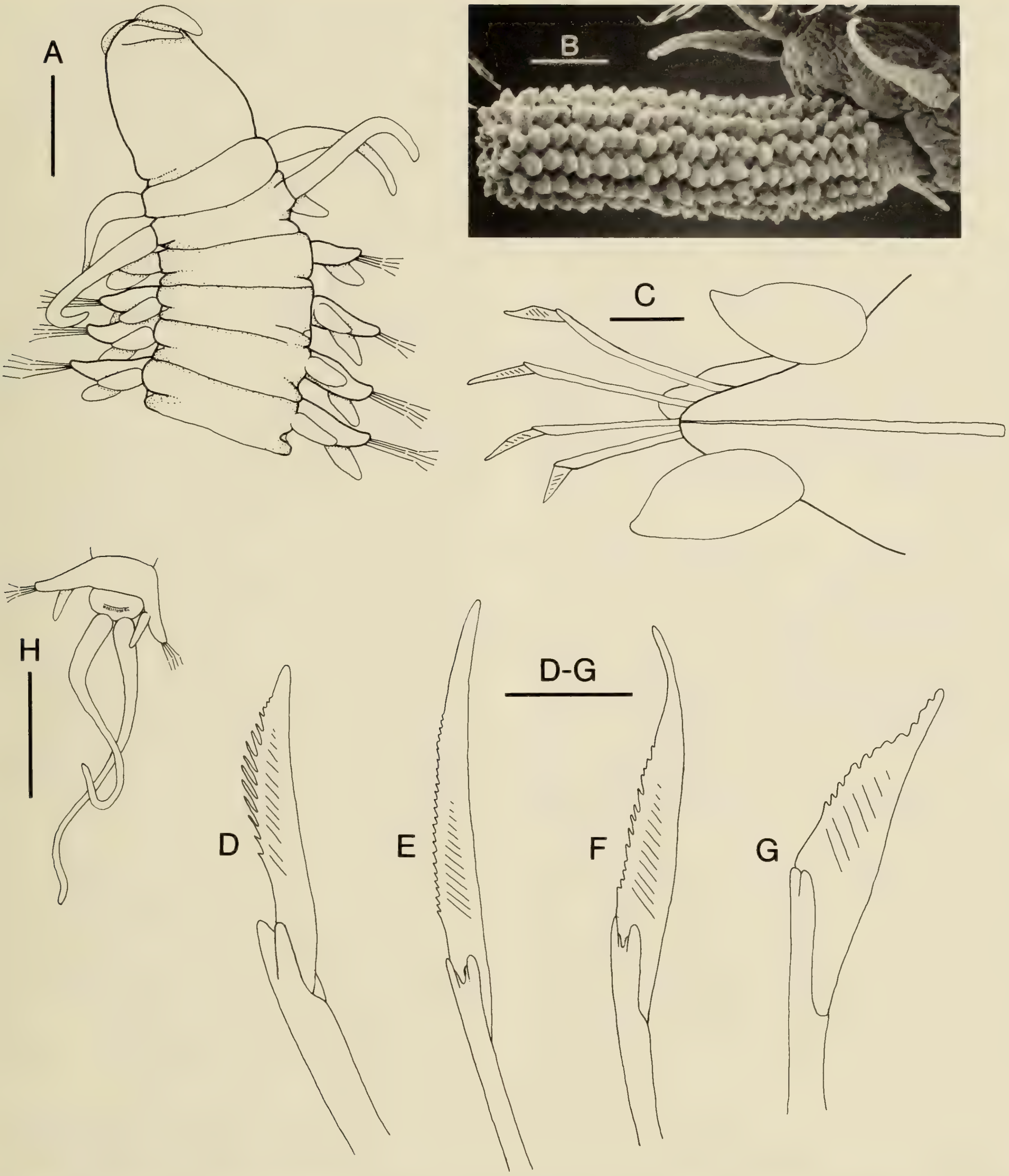

Fig. 1. *Hesionura coineaui* (Laubier, 1962). A. Anterior end, dorsal view. B. Proboscis, lateral view, SEM photograph. C. Parapodium of setiger 53 (from animal with 164 setigers), posterior view. D. Uppermost seta, lateral view. E. Next to uppermost seta, dorsolateral view. F. Next to lowermost seta, dorsolateral view. G. Lowermost seta, dorsolateral view. H. Pygidium with anal cirri, ventral view. A, D–G: DEJ-1, ZMUC. B, H: DEJ-22, ZMUC. C: DEJ-1, ZMUC. Scales: A = 0.1 mm; B = 50 μm; C = 25 μm; D–G = 10 μm; H = 0.1 mm. A, D–H redrawn from SEM photographs, D–G from same parapodium.

containing blue-green eggs (brown in alcohol) with diameter about 80 μm. Undisturbed living animals with very active movements.

Remarks.—These specimens have previously been reported (Eibye-Jacobsen 1991: 532) as *Hesionura elongata* (Southern, 1914), but they do not conform completely to any known species in this genus. Although very small eyes were present on living specimens, they have mostly faded in alcohol. This is probably also the case with many previous reports of this genus, in which living material may not have been observed. I regard the presence or absence of eyes as an unreliable character in *Hesionura.*

Judging from the original descriptions, setae of the type described here (i.e., all compound, uppermost seta trifid, remaining setae bifid, distal articles of same general length) are to be found only in *H. coineaui* (Laubier, 1962) and *H. fragilis* (Hartmann-Schröder, 1958). In *H. fragilis* the ventral cirri are very elongate, whereas the cirral morphology in *H. coineaui* resembles that shown here on Fig. 1C. Belizean animals differ from *H. coineaui* only in pigmentation (red according to Laubier). Furthermore, Laubier stated that the proboscideal papillae in *H. coineaui* are irregularly distributed. However, the fact that these papillae are arranged in longitudinal rows on the animals treated here was not recognized until they were studied using the SEM (Fig. 1B).

Hesionura elongata (Southern, 1914) was described from Ireland and has been reported from North Carolina (Day 1973, Gardiner 1975) and Massachusetts (Blake 1988). Gathof (1984) reported *Hesionura* sp. A from the Gulf of Mexico (Florida). Examination of the material studied by Gardiner (USNM 51018, 52870) and Gathof (USNM 89968, 89969, 89970), as well as unpublished specimens from South Carolina (USNM 56596, 59325, 59326) showed that the species involved was almost certainly the same as that found in Belize.

All of these worms, including those reported by Blake, differ from *H. elongata* as originally described and later reviewed by Hartmann-Schröder (1963), in having the uppermost seta trifid and all setae compound. However, in specimens from northern Europe this is also the case (pers. obs. using differential interference contrast microscopy; see also Pleijel & Dales 1991:66–67 as regards the uppermost seta). Some confusion with *H. augeneri* (Friedrich, 1937) may be involved, but it is unclear whether these two species are separate. I thus agree with Blake (1988:249) that an oversight may account for the description of this seta as bifid in *H. elongata.* However, in my opinion the North American animals cannot be referred to Southern's species, because they lack strongly elongate ventral cirri.

Distribution.—Belize: only taken around island of Carrie Bow Cay, in sand and *Halimeda* gravel, as well as in rubble of *Agaricia,* at depths of 0.6–12 m. Gulf of Mexico (Gathof 1984). South Carolina. North Carolina (Gardiner 1975). Massachusetts (Blake 1988)? Type locality: Racou, France, Mediterranean Sea (Laubier 1962).

Genus *Mystides* Théel, 1879

Mystides near *borealis* Théel, 1879

Mystides borealis.—Gathof 1984:19-10, fig. 19-6.—?Blake 1988:251, fig. 3a–b. [Not *Mystides borealis* Théel, 1879.]

Material examined.—DEJ-15 (1); DEJ-19 (1).

Description.—Unless otherwise noted based on specimen from st. DEJ-19. Length 5.2 mm, 0.35 mm wide excluding setae, with 49 segments (posteriorly incomplete). Specimen from st. DEJ-15: 3.0 mm long, 0.26 mm wide, with 39 segments (complete).

Prostomium round with 4 very thin filiform antennae, at least as long as prostomium, eyes large, dark red to black, possibly with lenses. Proboscis not everted.

Tentacular formula 1 + S 1/1 + S 0/N; all segments separate and fully developed, with vague segmental borders. Tentacular cirri all claviform with thin filiform tips; dorsal tentacular cirri of segment 2 longest.

Dorsal cirri oval, thick, with well-developed cirrophores. Neuropodia each with 6 or 7 setae. Setal rostrum with about 5 distal teeth. Ventral cirri oval, more elongate than dorsal cirri. Anal cirri resemble dorsal cirri of middle segments (DEJ-15); pygidial papilla not observed.

Living animals with colorless dorsum and venter. Dorsal, ventral, and tentacular cirri, and prostomium anterior to eyes with orange pigment and dark red spots, largest on dorsal and ventral cirri; several spots ventrally on segments 1–4 and on posterolateral portion of prostomium. Smaller specimen lighter colored with light yellow in place of orange pigment, only few reddish brown spots and dark red eyes. Pigmentation fades very little in alcohol. Larger specimen an immature male. Living animals with very slow movements.

Remarks.—Judging from the original description of *Mystides borealis,* the specimens from Belize differ in body length, number of setae per neuropodium (although both may be due to age differences), pigmentation, and the size of the eyes. Eyes are apparently smaller in *M. borealis* according to Théel (1879: fig. 29). Unfortunately, the type material of this species has been dried (Fredrik Pleijel, pers. comm.) and newly collected material from the type locality (Novaya Zemlya, Arctic Ocean) must be studied before worldwide reports can be correctly appraised.

The two specimens reported on here probably belong to the same species as that described by Gathof (1984) from the Gulf of Mexico as *Mystides borealis.*

Blake (1988:251–252, fig. 3a–d) reported on specimens from George's Bank (North Atlantic) which he referred to *M. borealis* Théel, 1879 and *M. caeca* Langerhans, 1880. The specimens from Belize agree with Blake's description of *M. borealis* in body dimensions, setal morphology, and the presence of eyes. They differ in lacking obvious lenses, in having dorsal cirri that are not flattened, and in having pigmentation more reminiscent of that described by Blake for *M. caeca* (i.e., with orange pigment).

The Belizean animals differ from the type specimens of *Mystides viridis* Webster & Benedict, 1887 (type locality: Eastport, Maine) in body proportions (thinner at a comparable length), pigmentation, the larger eyes, and the attachment of dorsal cirri to obvious cirrophores (Mary E. Petersen, pers. comm.).

Distribution.—Both specimens from Belize taken in sand samples from east of Carrie Bow Cay at depths of 4.5 and 16 m respectively. Northeastern Gulf of Mexico (Gathof 1984). North West Atlantic (Blake 1988)?

Genus *Phyllodoce* Lamarck, 1818
Phyllodoce erythrophylla (Schmarda, 1861)
Fig. 2

Lepadorhynchus erythrophyllus Schmarda, 1861:88, figs. a, b, pl. 29, fig. 232.

Phyllodoce (*Anaitides*) *erythrophylla.*—Augener 1925:23–24, 46.

Anaitides erythrophyllum.—Hartman 1944: 15.

Anaitides erythrophyllus.—Hartman 1951: 33.—Fauchald 1977:13.

Phyllodoce erythrophylla.—Mountford 1991:159–161, fig. 1a–c.

Phyllodoce cf. *erythrophylla.*—Eibye-Jacobsen 1991:535, fig. 2a.

Material examined.—R-23.4.74 (1); JDF-47-2 (1); GH-3 (1); GH-6 (1); GH-11 (3); GH-22 (1); GH-26 (1); GH-36 (2); GH-38 (4); AC-509 (3); AC-520 (3); K-35 (4); K-36 (3); K-43 (1); K-49 (3); K-62b (1); K-64 (1); K-70c (1); K-74 (2); K-96 (1); K-107 (1); RC-1 (1); RC-5 (1); RC-7 (1); RC-15 (1); RC-26 (1); RC-32 (1); RC-33 (1); RC-34 (1); RC-37 (1); RC-39 (2); RC-40 (2); RC-59 (1); RC-80 (1); RC-82 (1); RC-92 (2); RC-93 (1); RC-94 (1); RC-98 (1); RC-100 (2); RC-119 (1); F-65 (1); F-116 (1); F-265 (1); F-269 (4); F-275 (1); F-279 (1); F-282 (4, 2 used for SEM); DEJ-6 (1); DEJ-12 (1); DEJ-17 (1).

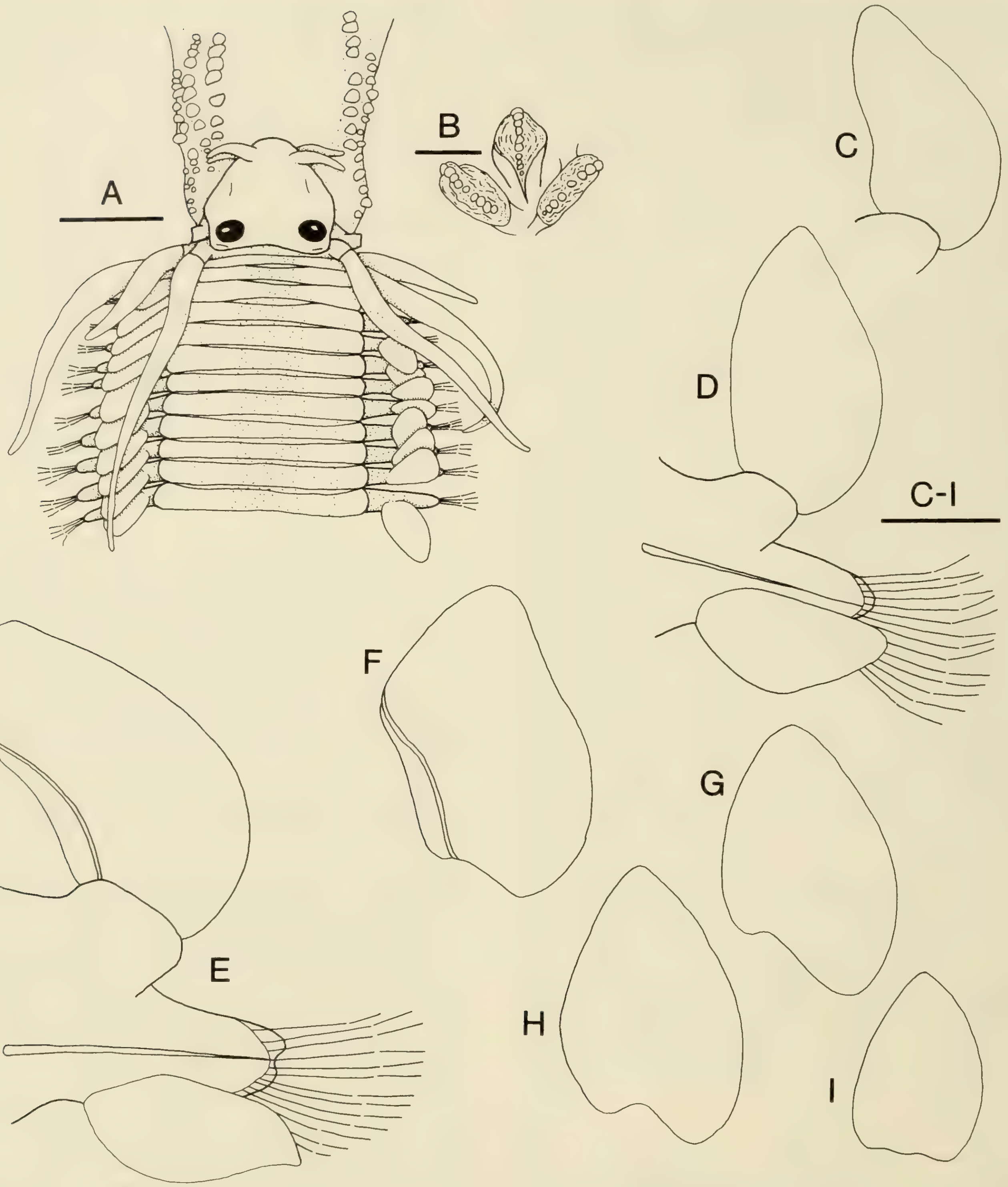

Fig. 2. *Phyllodoce erythrophylla* (Schmarda, 1861). A. Anterior end, dorsal view (rows of papillae on proboscis appear merged from this angle). B. Three oral papillae. C. Dorsal cirrus of setiger 6. D. Parapodium of setiger 36, posterior view. E. Parapodium of setiger 75, posterior view. F. Dorsal cirrus of setiger 89. G. Dorsal cirrus of setiger 122. H. Dorsal cirrus of setiger 137. I. Dorsal cirrus of setiger 222. A, C–I: F-279, USNM. B: F-282, USNM. Scales: A = 0.5 mm; B = 0.1 mm; C–I = 0.25 mm. B redrawn from SEM photograph.

Description.—Unless otherwise noted based on specimen from st. F-279. Length 54 mm, width excluding setae 1.6 mm, with about 270 setigers (animal almost complete).

Prostomium pentagonal or cordiform, slightly broader than long; nuchal papilla visible on most specimens (concealed on specimen from st. F-279; Fig. 2A) in median dorsoposterior concavity; 4 antennae present, all subulate and very short; eyes oval, dark red on living animals, dark reddish brown after preservation, with well-developed lenses; nuchal organs lateral, just anterodorsal to cirrophores of first pair of tentacular cirri.

Basal sixth of everted proboscis with 6 longitudinal rows of papillae on each side, without mediodorsal row; each row with up to 13 papillae (e.g., from dorsal to ventral: 10, 12, 13, 12, 10, and 12 on right side—9, 12, 12, 11, 10, and 10 on left side); individual papillae light reddish brown, pigmentation strongest on posterior surfaces; papillae compressed (about 60 × 25 μm) with posterior surface appearing glandular (irregularly convoluted as viewed in SEM); distal $^5\!/_6$ of proboscis with 6 longitudinal rows of large rounded tubercles, ventral ones most strongly developed; distal opening surrounded by 17 (rarely 16) oral papillae, each laterally compressed (about 140 by 50 μm) with medial row of about 10 wartlike structures (15–20 μm in diameter) along exterior and distal surface (Fig. 2B).

Tentacular formula 1 + 0 1/1 + 0 1/N; all segments separate; setae from segment 4. Dorsal portion of segment 1 and part of segment 2 covered by posterior part of prostomium. Tentacular cirri subulate, with those of segment 1 and ventral cirri of segment 2 reaching posteriorly to segment 8–9; dorsal cirri of segment 2 longest, reaching to segment 14–16; dorsal cirri of segment 3 reaching to segment 12–13 (n = 13). On specimens with everted proboscides dorsal cirri of segment 3 arising more ventrally than ventral cirri of segment 2.

Dorsal cirri of following segments changing markedly in shape along body; those of anterior segments blunt, asymmetrically lanceolate (Fig. 2C–D), gradually becoming quadrangular with ventral/outer margins longest (Fig. 2E), then shortening towards middle of body (Fig. 2F), before becoming blunt, asymmetrically cordiform (Fig. 2G–H), and finally almost symmetrical (Fig. 2I). Dorsal cirri from about segment 15 with strongly developed cirrophores and single ciliary bands along inner margins of posterior surfaces; latter most easily seen on middle segments (Fig. 2E–F). Supra-acicular lip of neuropodial presetal lobe larger and longer than sub-acicular lip, especially on middle and posterior segments. Neuropodium with up to 18 setae; rostrum of setal shaft with well developed heel and many acuminate teeth, increasing in size toward tip (see Eibye-Jacobsen 1991: fig. 2a, SEM photograph). Ventral cirri longer than neuropodium throughout; oval to triangular with tip pointing laterally on anterior segments (Fig. 2D), ventrolaterally on middle and posterior segments (Fig. 2E). Anal cirri not observed.

Living animals yellowish with brown pattern on dorsum; pigment on anterior segments concentrated medially, forming broad diffuse mediodorsal longitudinal band, becoming weaker on middle segments (concentrated medially between segments and mediolaterally on each segment; "checkerboard" pattern), and weaker still on posterior segments, predominantly distributed along medial posterior edge of each segment. Prostomium pale apart from dark brown area at each posterolateral corner (Fig. 2A). Dorsal cirri on anterior segments pale, gradually becoming dark yellow or reddish, then reddish brown on posterior segments. Venter, ventral cirri and neuropodia pale. Brown pattern on dorsum becoming very dark on preserved animals, often almost black, dorsal cirri becoming yellowish orange on middle segments, reddish brown on posterior segments.

Remarks.—Mountford (1991) studied the type material of *P. erythrophylla* and a large number of specimens from various localities in the Atlantic Ocean, Gulf of Mexico, Caribbean Sea, and Western Pacific. She recognized Schmarda's species for the holotype only, taken off the south coast of Jamaica, and referred all other material to *P. madeirensis* Langerhans, 1880.

Mountford separated *P. madeirensis* from

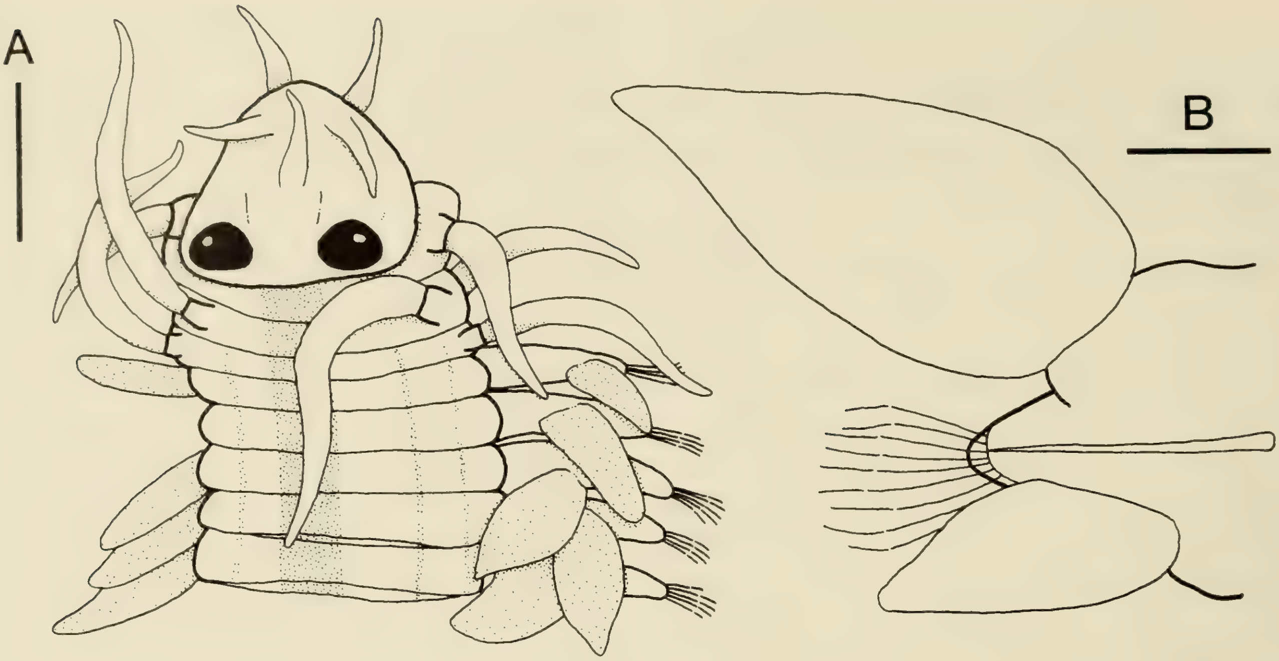

Fig. 3. *Eulalia myriacycla* (Schmarda, 1861). A. Anterior end, dorsal view. B. Parapodium of setiger ca. 250 (from animal with about 530 setigers), posterior view. DEJ-13, ZMUC. Scales: A = 0.25 mm; B = 0.1 mm.

P. erythrophylla exclusively on the presence of brown transverse bands on the dorsum of the former, lacking on the latter, as well as the reported color of live animals. However, her information on the pigmentation of live specimens (dorsum purple, dorsal cirri red) is taken from the original description. According to Langerhans (1880:308), live *P. madeirensis* are colorless as juveniles, dull green as adults. Although living specimens from Belize have a coloration unlike either of these descriptions, preserved animals correspond well to Mountford's description of *P. madeirensis*. Schmarda may have exaggerated the brilliance of pigmentation on his specimen of *P. erythrophylla,* as on several other of the worms shown in his plates.

In my opinion, the Belizean animals most closely resemble Schmarda's species because of their consistent lack of a mediodorsal row of papillae on the proximal part of the proboscis (n = 35). Such a row, containing about six papillae, is present in *P. madeirensis* (Langerhans 1880:308). Gathof (1984:39) reported that his specimens of *P. madeirensis* from the Gulf of Mexico lacked this mediodorsal row. However, examination of a voucher specimen (USNM 89986) showed it to be present. These papillae are also present on specimens from North Carolina (Gardiner 1975:115 and fig. 7q). Much confusion still exists as to the true identity of *P. erythrophylla* and its correct separation from *P. madeirensis* (see discussion in Mountford 1991:165–166).

Distribution.—Found in Belize in rubble of *Agaricia agaricites, Acropora cervicornis,* and *Porites porites* at depths of 0–36 m. Further reports from the Caribbean Sea: southern Jamaica, on coral reef (Schmarda 1861: 88); Colombia, Bahia Honda (Hartman 1944:15); Panama, Galeta Reef (Fauchald 1977:13). Also reported from southern Florida in the Gulf of Mexico, associated with reefs (Hartman 1951:33).

Genus *Eulalia* Savigny, 1822
Eulalia myriacycla (Schmarda, 1861)
Fig. 3

Notophyllum myriacyclum Schmarda, 1861: 87, figs. a, b, pl. 29, fig. 233.
Myriocyclum schmardae Grube, 1880:208.
Eulalia myriacycla.—Augener 1925:24–25, 46.

Eulalia myriacyclum.—Hartman 1944: 16.—Hartman 1951:33–34.—Fauchald 1977:14.

Eulalia quinquelineata Treadwell, 1901:192, figs. 27–29.—Treadwell 1924:9.

Material examined.—R-23.4.74 (2); R-2.5.74-2 (2); R-4.5.74-3 (1); JDF–23-2 (1); RC-98 (fragment); F-45 (1); F-48 (1); F-116 (fragment); F-279 (1); DEJ-4 (1); DEJ-13 (1): DEJ-20 (1).

Description.—Unless otherwise noted based on specimen from st. DEJ-13. Length 110 mm (specimen from st. JDF-23-2 about 150 mm long), width excluding setae and dorsal cirri 0.7 mm, with about 530 setigers.

Prostomium rounded conical, slightly broader than long (Fig. 3A). Five antennae present, all of same length, median one inserted halfway between eyes and anterior border of prostomium. Eyes large, dark red on living animals, reddish brown after preservation, with well-developed lenses. Proboscis densely covered with diffusely distributed papillae (diameter about 30 μm); oral papillae not observed.

Tentacular formula 1 + 0 1/1 + 0 1/N; setae present from segment 4 on large individuals, from segment 3 on smaller animals (e.g., specimen from st. DEJ-20, about 15 mm long); all segments separate and fully developed dorsally. Tentacular cirri subulate, except ventral ones of segment 2, which may be slightly flattened; cirri of segment 1 and ventral cirri of segment 2 reaching to segment 5, dorsal cirri of segments 2 and 3 reaching to segment 8.

Dorsal cirri of middle segments elongate cordiform to lanceolate, distally acuminate (Fig. 3B), on anterior segments less and on posterior segments more elongate. Neuropodial presetal lobe with poorly developed supra- and sub-acicular lips, more or less conical. Neuropodia of middle segments each with 7 to 9 setae. Setal rostrum strongly inflated, without heel, with 2 large distal teeth, of the *E. viridis* type (see Eibye-Jacobsen 1991:537). Distal article of seta short and slender. Ventral cirri triangular, almost acuminate distally, longer than neuropodium (Fig. 3B). Anal cirri elongate oval, distally rounded, and slightly flattened, about 4 times longer than broad. Pygidial papilla absent.

Living animals yellowish with 5 dark brown to black longitudinal lines on dorsum (Fig. 3A), pattern becoming weaker posteriorly; median line strongest, mediolateral lines weakest. Similar pattern present on venter, although weaker and lacking mediolateral lines. Dorsal, ventral, and anal cirri yellow, often densely covered with small dark reddish brown pigment spots, especially concentrated distally. Pigmentation fades only slightly on preserved animals.

Remarks.—In the original description of this species, Schmarda (1861:87) indicated that four eyes and four antennae were present. Both points were corrected by Augener (1925:25) after study of the two type specimens. According to Fredrik Pleijel (in litt.) this material, which was deposited in the Zoological Institute of Vienna, may now be lost. Augener's case for the synonymy of Schmarda's species and *E. quinquelineata* Treadwell, 1901 is very convincing, and was also followed by Hartman (1951:33). The holotype of *E. quinquelineata* (Puerto Rico: Hucares, 13 Feb 1899, S/S *Fish Hawk*, USNM 15922) resembles exactly the original illustration of *Eulalia myriacycla* (Schmarda 1861: pl. 29, fig. 233) and clearly belongs to the same species as that taken in Belize.

Schmarda had a specimen that was over 300 mm long with 1020 segments, whereas the holotype of *E. quinquelineata* is even larger, 450 mm long with "at least 1,300 segments" (Treadwell 1901:192).

The genus *Myriocyclum* [sic] was erected by Grube (1880:208) for *Notophyllum myriacyclum* Schmarda based on characters later proven to be incorrectly observed (Augener 1925:24–25). Grube renamed the species *M. schmardae*. In agreement with Hartman (1959:155), *Myriocyclum* is here considered a junior synonym of *Eulalia* and *M. schmardae* a junior synonym of *E. myriacycla.*

In the original illustration (fig. 28) of a parapodium of *E. quinquelineata,* the size of the neuropodial presetal lobe and ventral cirrus and the shape of both these organs and that of the dorsal cirrus are misrepresented (checked on holotype). These organs match closely the original description of *E. myriacycla* and Fig. 3B here.

Young & Young (1982:119) reported a single specimen of *E. viridis* (Linnaeus, 1767) from the lagoon east of Carrie Bow Cay. No details were given and I have not had the opportunity to study the specimen. This report may refer to *E. myriacycla,* as it is of a similar size and general appearance, although it differs noticeably in pigmentation.

Distribution.—Found in Belize in rubble of *Acropora palmata* and *Porites porites* at depths of 0–16 m. Further reports from the Caribbean Sea: Jamaica, on coral reef (Schmarda 1861:87); Puerto Rico, Hucares (Treadwell 1901:192); Lesser Antilles (Treadwell 1924:9); Venezuela, Cubagua Island (Hartman 1944:5); Panama, Galeta Reef (Fauchald 1977:14). Also reported from the Gulf of Mexico (southern and northwestern Florida), associated with reefs (Hartman 1951:33–34).

Genus *Eumida* Malmgren, 1865

Eumida muriatica, new species

Fig. 4

Eumida sp.3 Eibye-Jacobsen, 1991:532, fig. 2b.

Material examined.—GH-36 (3); K-33 (1); K-36 (1); K-43 (2); K-47 (2); K-53 (1); K-107 (1); RC-1 (13); RC-3 (7); RC-6 (2); RC-7 (1); RC-8 (7); RC-9 (1); RC-10 (1); RC-12 (1); RC-17 (1); RC-19 (2); RC-32 (1); RC-34 (1); RC-36 (fragment); RC-40 (1); RC-52 (3); RC-53 (4); RC-56 (2); RC-59 (1); RC-80 (1); RC-83 (1); RC-90 (1); RC-91 (3); RC-92 (8); RC-93 (4); RC-94 (14); RC-95 (5); RC-96 (3); RC-97 (1); RC-98 (6); RC-99 (4); RC-100 (11); RC-111 (5); RC-112 (5); RC-113 (4); RC-114 (2); RC-115 (3); RC-116 (4); RC-117 (10); RC-118 (3); RC-119 (4); RC-120 (1); F-4 (1); F-25 (1); F-30 (1); F-35 (1); F-44 (3); F-45 (9); F-274 (1 paratype, USNM 144859); F-283 (1 paratype, USNM 144860); DEJ-3 (1 paratype, ZMUC); DEJ-4 (holotype + 19 paratypes, ZMUC; 15 paratypes, USNM 144861); DEJ-7 (13 paratypes of which 2 used for SEM, ZMUC); DEJ-14 (5 paratypes, ZMUC); DEJ-16 (2 paratypes, ZMUC); DEJ-17 (2 paratypes, ZMUC).

Description.—Holotype complete, 2.4 mm long, 0.5 mm wide without setae, with 31 setigers. Other complete specimens up to 4.2 mm long, up to 0.6 mm wide without setae, with up to 39 setigers.

Prostomium circular with straight dorsoposterior margin, about a third broader than long (Fig. 4A); 5 antennae present, all basally swollen and distally drawn out into long thin tips; frontal antennae widely spaced, with dorsal ones almost as long as prostomium, ventral ones slightly shorter (Fig. 4B); median antenna longest, inserted anteriorly between eyes. Eyes very large, red, darker along anterior and medial edges, with lenses (Fig. 4A).

Proboscis not everted on holotype, observed on several paratypes; distal ¾ of length with well spaced, irregularly distributed, obvious micropapillae (4–5 μm in diameter); proximal ¼ with larger (8–10 μm in diameter) and more densely placed micropapillae (Fig. 4C); oral papillae not observed.

Tentacular formula 1 + S 1/1 + S 1/N; segment 1 dorsally and to some extent ventrally reduced, clearly delineated from segment 2; segment 2 slightly reduced dorsally. All tentacular cirri fusiform, basally swollen and distally drawn out, except ventral tentacular cirri of segment 2 (tip only weakly drawn out); those of segment 1 and ventral cirri of segment 2 reaching to segment 5, dorsal cirri of segment 2 longest, reaching to segment 8, as do dorsal cirri of segment 3.

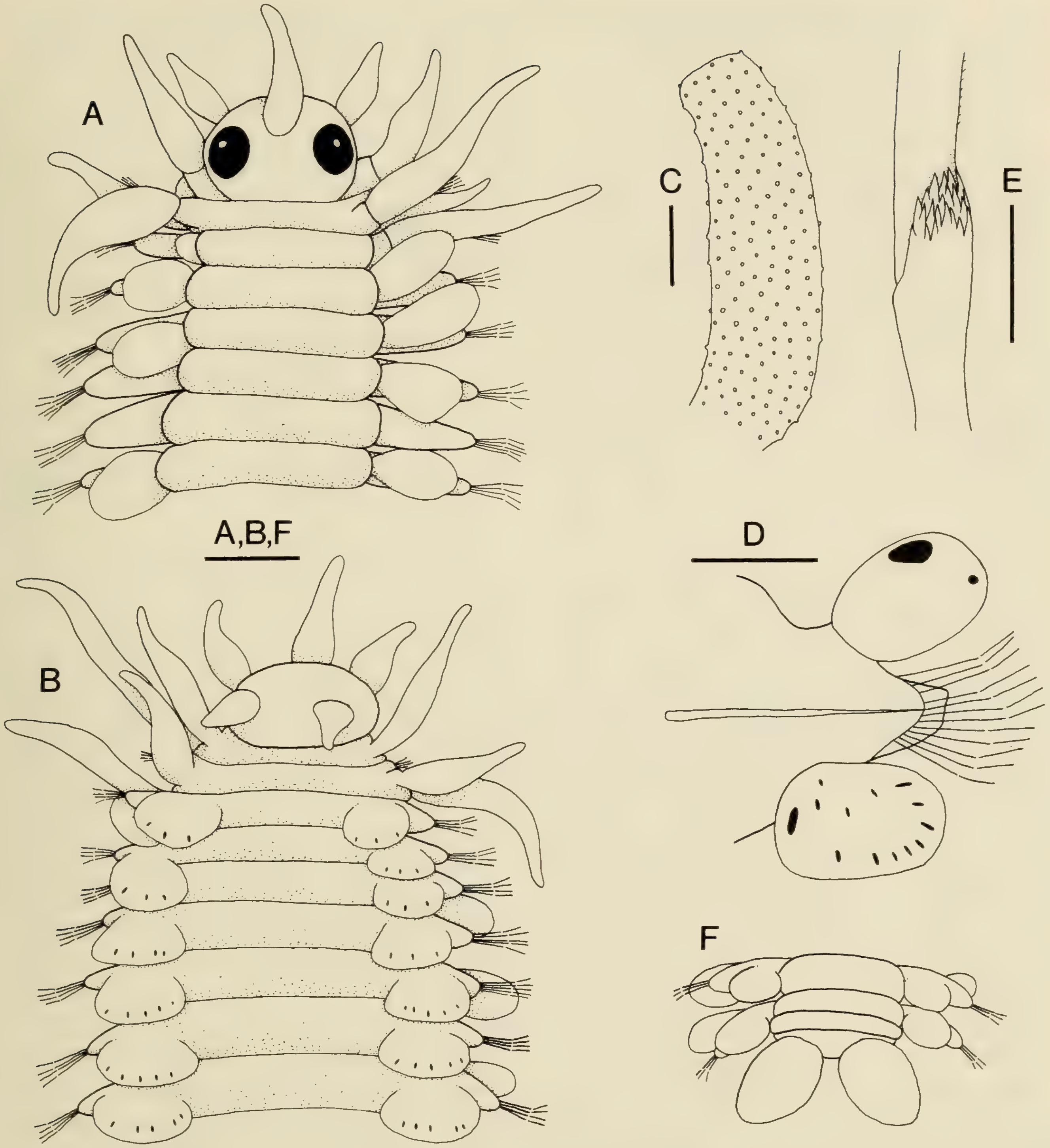

Fig. 4. *Eumida muriatica,* new species. A. Anterior end, dorsal view. B. Anterior end, ventral view. C. Everted proboscis, lateral view. D. Parapodium of setiger 17 (from animal with 39 setigers), posterior view. E. Seta at region of articulation. F. Posterior end with pygidium and anal cirri, ventral view. A–B, E–F: holotype, ZMUC. C–D: paratype, DEJ-4, ZMUC. Scales: A–B, F = 0.1 mm; C = 0.1 mm; D = 0.1 mm; E = 5 μm.

All dorsal cirri similar; thickened oval to rectangular, slightly asymmetrical, distally blunt, almost 1½ times as long as broad (Fig. 4D). Supra-acicular lip of neuropodial presetal lobe slightly longer than sub-acicular lip. Rostrum of setal shaft with well developed heel and apical crown of 15–20 teeth (Fig. 4E; see also Eibye-Jacobsen 1991: fig. 2b, SEM photograph); distal article of seta rather short. All ventral cirri similar; slightly larger than dorsal cirri, thickened oval, distally blunt, about 1½ times as long as broad, not projecting beyond neuropodial tips (Fig. 4D). Anal cirri thickened oval, distally blunt, 1½ to 2 times as long as broad (Fig. 4F). Pygidial papilla absent.

Living animals with yellowish green tinge; each segment with small green spots in broad diffusely defined transverse band dorsally (becomes dark brown in alcohol). Dorsal cirri pale yellow; on most specimens each with dark brown spot at dorsal edge (Fig. 4D). Ventral cirri darker, with 10 to 15 relatively large orange-red spots (glands?) predominantly along ventral edge (Fig. 4B, D). Dark reddish brown blotches of pigment often irregularly distributed on prostomium.

No ovigerous females recognized: 2 paratypes (3.5 mm long with 35 setigers, from st. DEJ-4) appear to contain sperm.

Remarks.—This species is referred to *Eumida,* although the cirral morphology and large eyes are not typical of the genus. However, similar structures may be found in *E. subulifera* (Ehlers, 1897) and, as regards the cirri, *E. minuta* (Ditlevsen, 1917). These species have important characters in common with both *Eumida* and *Clavadoce* Hartman, 1936 and a final decision on where they should be placed is deferred until our knowledge of the latter is more complete.

Eumida muriatica, n. sp. most closely resembles *E. subulifera* (Ehlers, 1897), both species having, in addition to the points mentioned above, a row of orange-red glandlike spots along the ventral edge of the ventral cirri (Fig. 4D). The species described here differs from *E. subulifera* in its lack of a pygidial papilla and proboscideal macropapillae (30–40 μm in diameter in the latter), in the presence of a large spot of pigment on the dorsal cirri, in having ventral cirri which are slightly larger than the dorsal cirri, and in the more or less horizontal (rather than obliquely upward) attachment of the ventral cirrus to the neuropodium.

Etymology.—This species is named for its yellowish green color (muriaticus is Latin for pickled).

Distribution.—Found in coral rubble (*Porites, Acropora palmata,* and *A. cervicornis*) and among bunches of *Halimeda, Padina,* and *Dictyota dichotoma* at depths of 0–18 m. Known only from Belize: around Carrie Bow Cay in all directions, at South Water Cay, at the Cocoas, and at the Sand Bores. Type locality: in lagoon, about 50m north of Carrie Bow Cay, Belize, 0.5 m, in rubble of *Porites.*

Genus *Sige* Malmgren, 1865
Sige belizensis, new species
Fig. 5

Sige sp. 2 Eibye-Jacobsen, 1991:532, fig. 2c–d.

Material examined.—AC-520 (1); K-37 (3); K-49 (1); K-55 (3); K-60T (1); K-66 (1); K-70b (1); K-77 (3); K-101 (1); RC-1 (1); RC-12 (1); RC-17 (3); RC-26 (2); RC-31 (1); RC-35 (1); RC-36 (1); RC-37 (3); RC-39 (1); RC-40 (1); RC-45 (1); RC-50 (1); RC-53 (1); RC-56 (2); RC-94 (1); RC-95 (1); RC-96 (3); RC-97 (1); RC-98 (12); RC-99 (1); RC-100 (9); RC-105 (2); RC-107 (2); RC-108 (2); RC-111 (15); RC-112 (2); RC-113 (9); RC-114 (8); RC-115 (7); RC-116 (8); RC-117 (7); RC-118 (1); RC-119 (3); RC-120 (5); F-1 (1); F-27 (2); F-35 (1); F-42 (1); F-45 (2); F-147 (1); F-263 (2 paratypes, USNM 144862); F-266 (1 paratype, USNM 144863); F-275 (3 paratypes, USNM 144864); F-278 (1 paratype, USNM 144865); F-281 (3 paratypes, USNM 144866); F-285 (3 paratypes, USNM 144867); DEJ-3 (1 paratype, ZMUC); DEJ-4 (18 paratypes, ZMUC; 15 paratypes, USNM 144868); DEJ-6 (1 paratype, ZMUC); DEJ-7 (21 paratypes, ZMUC); DEJ-12 (2 paratypes, ZMUC); DEJ-13 (1 paratype, ZMUC); DEJ-14 (holotype + 5 paratypes of which 1 used for SEM, ZMUC; 5 paratypes, USNM 144869); DEJ-17 (4 paratypes, ZMUC); DEJ-18 (3 paratypes, ZMUC).

Description.—Holotype complete except for anal cirri, 2.7 mm long, 0.6 mm wide

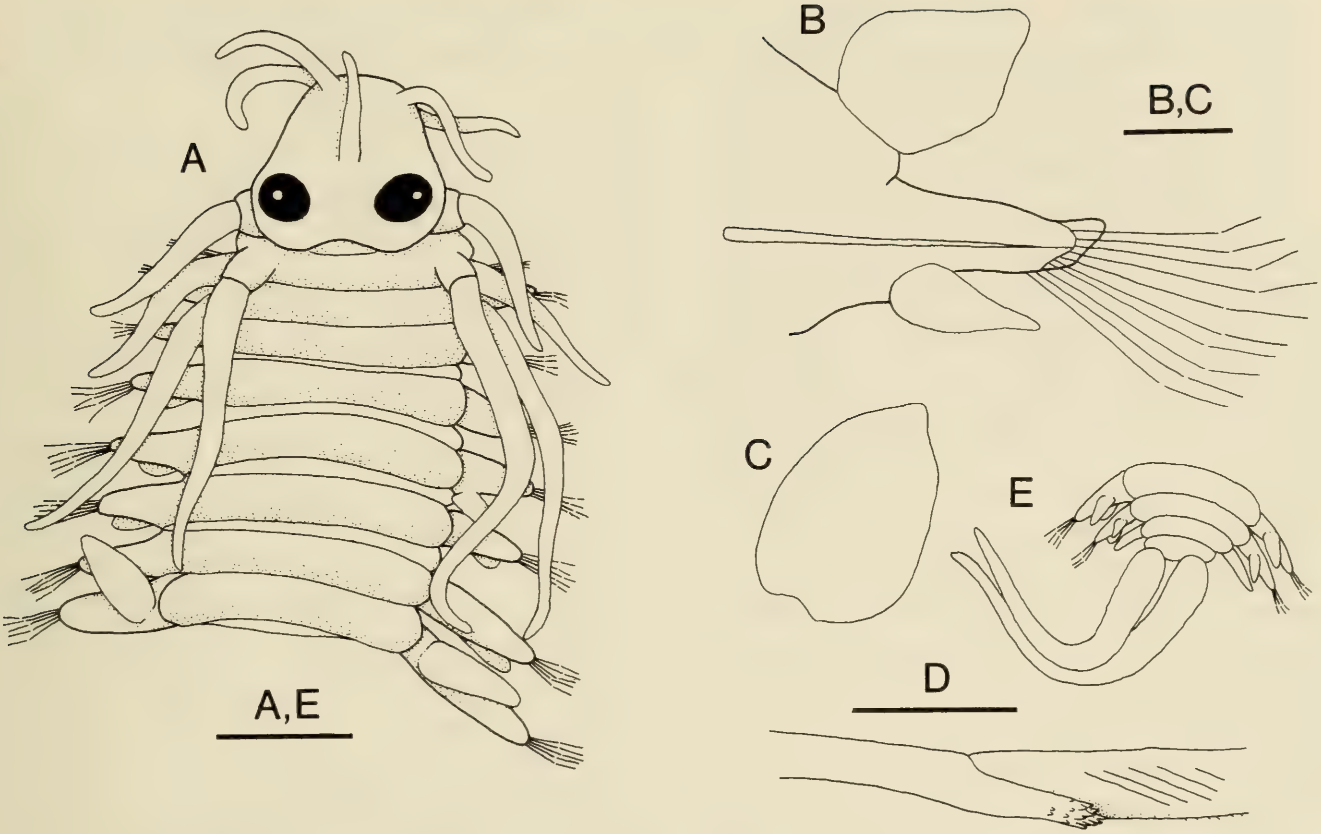

Fig. 5. *Sige belizensis,* new species. A. Anterior end, dorsal view. B. Parapodium of setiger 18, posterior view. C. Dorsal cirrus of setiger 9 (from animal with 52 setigers). D. Seta at region of articulation. E. Posterior end of body with anal cirri, ventral view. A–B: holotype, ZMUC. C: paratype, DEJ-17, ZMUC. D–E: paratypes, DEJ-14, ZMUC. Scales: A, E = 0.1 mm; B–C = 50 μm; D = 5 μm. D redrawn from SEM photograph.

without setae, with 36 setigers. Other, complete specimens up to 10.0 mm long (DEJ-4), up to 1.0 mm wide without setae (mature females, e.g., DEJ-17), with up to 52 setigers.

Prostomium cordiform to pentagonal, distinctly concave posteriorly, slightly broader than long (Fig. 5A). Five subulate antennae present, slightly shorter than prostomium; median antenna may be shorter and narrower, inserted between or just anterior to eyes. Eyes large, red in life, dark red or reddish brown on preserved animals, with lenses (Fig. 5A). Nuchal organs well-developed, situated on edge of prostomium behind eyes (studied in SEM).

Proboscis smooth with few widely spread micropapillae; 17 oral papillae, each with micropapillae (paratype from DEJ-14).

Tentacular formula 1 + S 1/1 + S 1/N; segment 1 partially reduced dorsally, visible in posterior concavity of prostomium, clearly separate from segment 2 (Fig. 5A). All tentacular cirri cirriform, with those of segment 1 reaching to segment 5, those of segment 2 reaching to segment 6, and dorsal cirri of segments 2 and 3 reaching to segment 9 or 10 (holotype, tentacular cirri proportionately longer on larger specimens).

Dorsal cirri on middle segments asymmetrically cordiform, about 1⅓ times as long as broad (Fig. 5B); cirri of posterior segments similar, but more elongate, cirri of anterior segments almost oval (Fig. 5C). Supra-acicular lip of neuropodial presetal lobe prolonged and much larger than sub-acicular lip (Fig. 5B). Rostrum of setal shaft weakly inflated, with well-developed heel and very few, distally placed, teeth (Fig. 5D); distal article of seta long. Ventral cirri on anterior and middle segments lanceolate, about twice as long as broad, shorter than neuropodium (Fig. 5B); slightly more elongate on posterior segments. Anal cirri observed on several paratypes as cirriform, about 10 times as long as broad (Fig. 5E); pygidial papilla absent.

Living animals pale yellow with light orange-brown dorsal and ventral cirri; tentacular cirri and prostomium anterior to eyes can have same color; dorsal cirri on many specimens with dark orange-brown pigment (glands?) along dorsal and ventral edges, not reaching tip; ventral cirri can also have this pigment. Preserved animals colorless apart from dorsal and ventral cirri.

Type material includes many mature specimens. Males and females as small as 3.0 mm, with about 35 setigers, may contain sexual products. Eggs yellowish green (light reddish brown in alcohol), up to 100 μm in diameter, with a visible germinal vesicle from a diameter of about 70 μm.

Remarks.—According to Pleijel (1990), the genus *Sige* contains ten species, only four of which possess eyes. *Sige belizensis* most closely resembles *S. parvicirrus* (Perkins, 1984), especially in the shape of the dorsal cirri. Study of the type material (USNM 80510) shows, however, that it differs from *S. belizensis* in having a much broader prostomium, relatively shorter antennae and tentacular cirri, smaller eyes, and darker pigmentation. Furthermore the large, brown "brain lobes," which are characteristic of *S. parvicirrus,* are absent in *S. belizensis.*

Etymology.—This species is named after the beautiful country from which it is described.

Distribution.—Found in coral rubble (*Porites, Acropora palmata,* and *A. cervicornis*) and among bunches of *Amphiro, Dictyota, Caulerpa racemosa,* and *Halimeda,* at depths of 0–28 m. Known only from Belize (around Carrie Bow Cay, South Water Cay, Tobacco Cay, and the Sand Bores). Type locality: in lagoon, 50 m south of Carrie Bow Cay, Belize, 0.3 m, in rubble of *Porites.*

Genus *Pterocirrus* Claparède, 1868

Pterocirrus foliosus (Treadwell, 1924)

Fig. 6

Eulalia foliosa Treadwell, 1924:10, pl. 2, figs. 16–18.

Pterocirrus foliosus.—Eibye-Jacobsen 1991: 532, fig. 2e.

Sige orientalis?—Fauchald 1977:16. [Not *Sige macroceros orientalis* Imajima & Hartman, 1964.]

Material examined.—R-23.4.74 (3); JDF-15-3 (1); GH-16 (1); GH-26 (1); GH-36 (4); K-35 (4); K-36 (3); K-55 (4); K-60T (4); K-98 (2); RC-7 (2); RC-10 (1); RC-18 (2); RC-28 (1); RC-30 (1); RC-33 (2); RC-52 (1); RC-61 (2); RC-62 (1); RC-63 (1); RC-76 (1); RC-81 (1); RC-83 (fragment); RC-85 (1); RC-86 (1); RC-87 (1); RC-90 (2); RC-101 (1); F-4 (4); F-21 (1); F-30 (1); F-44 (1); F-45 (6); F-116 (3); F-135 (1); F-261 (2); F-263 (3); F-266 (15); F-270 (9); F-282 (1); DEJ-3 (1); DEJ-4 (4, 1 used for SEM); DEJ-6 (7); DEJ-7 (2); DEJ-10 (1); DEJ-12 (8, 1 used for SEM); DEJ-13 (7); DEJ-14 (7); DEJ-18 (3); DEJ-21 (2).

Description.—Length up to 24 mm (DEJ-21, posteriorly incomplete), most specimens 5–10 mm long. Width without setae up to 3.0 mm, on 10.7 mm long specimen 1.2 mm (F-270). Up to 90 setigers (DEJ-21), 10.7 mm long specimen with 78 setigers.

Prostomium rounded, broader than long, with wedge-shaped or rectangular dorsoposterior depression (Fig. 6A); 5 subulate antennae present, each almost as long as prostomium; median antenna may be slightly thinner, inserted anteriorly just in front of eyes. Eyes very large, circular or oval, dark red in life (even darker in preserved specimens), with lenses. Nuchal organs small, situated on posterior edge of prostomium.

Proboscis densely covered with diffusely distributed, elongate conical papillae; each about 40 μm long and 15 μm wide, with an

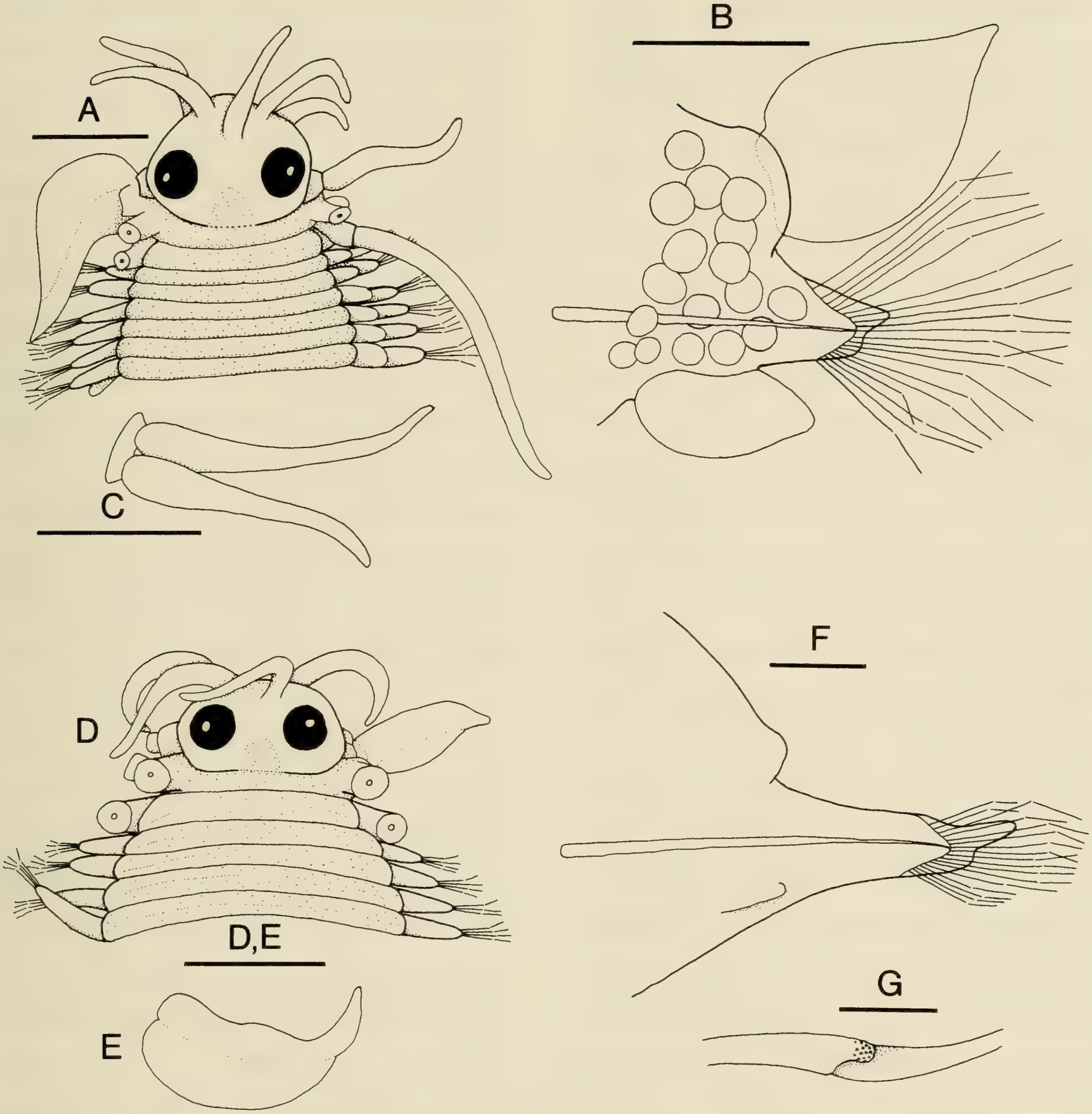

Fig. 6. *Pterocirrus foliosus* (Treadwell, 1924). A. Anterior end, dorsal view. B. Parapodium of setiger 43 (from animal with 80 setigers), posterior view. C. Pygidium with anal cirri, dorsal view. D. Anterior end, dorsal view. E. Ventral tentacular cirrus of segment 2, dorsolateral view. F. Parapodium of setiger 48, posterior view, dorsal and ventral cirri lost. G. Seta at region of articulation. A–B: F-270, USNM. C: F-261, USNM. D–G: holotype, USNM 20328. Scales: A = 0.25 mm; B = 0.25 mm; C = 0.25 mm; D–E = 0.5 mm; F = 0.25 mm; G = 25 μm.

apical ring of 6 (?) pores (diameter of each about 0.4 μm, observed in SEM).

Tentacular formula 1 + 0 1/1 + 0 1/N; neuropodium of segment 3 diminutive, setae present from segment 4; segment 1 dorsally reduced (but see remarks below), segments 1 and 2 ventrally fused, with longitudinal furrows. Tentacular cirri cirriform, except ventral ones of segment 2 which each bear a large ventral lamella (Fig. 6A); tentacular cirri of segment 1 reaching to segment 7, ventral cirri of segment 2 reaching to segment 8, dorsal cirri of segments 2 and 3 reaching to segment 12.

Dorsal cirri of middle segments elongate, cordiform, with drawn-out acuminate tip, asymmetrical with ventral margin longest, about 1½ times as long as broad (Fig. 6B); cirri of anterior segments less elongate, and cirri of posterior segments lanceolate, about twice as long as broad. Supra-acicular lip of neuropodial presetal lobe drawn out to a sharp tip, especially long on larger specimens. Rostrum of setal shaft with small, apically concentrated teeth, otherwise smooth, with well-developed heel (Fig. 6G; verified also on animals from Belize using SEM); upper setae in fascicle with narrower rostrum and fewer teeth, lower setae with more truncate rostrum. Distal article of seta long. All ventral cirri similar, elongate oval with blunt tip, considerably shorter than neuropodium (Fig. 6B), on larger specimens tip more acuminate, pointing slightly downwards. Anal cirri cirriform, about 6 times as long as broad (Fig. 6C); pygidial papilla absent.

Living animals pale brown or greenish with broad brown dorsal longitudinal band; brown pigment also present on dorsoposterior depression of prostomium and often on antennae and pygidium; dorsal and ventral cirri with reddish brown pigment; pigment often also present on venter as weak, transverse, segmental bands. Brown color of dorsum becoming darker on preserved animals, nearly black on large ones. On most specimens single thin light ciliary band evident across dorsum of most segments.

Material includes mature specimens; smallest complete recognizable male 4.8 mm long, smallest complete female containing eggs 7.4 mm long (F-270). Eggs dark olive-green (dark brown or reddish brown in alcohol), up to 70 μm in diameter (not quite mature, DEJ-14).

Remarks.—*Eulalia foliosa* was originally described from a single specimen from Barbados (Treadwell 1924) and has not been reported since. Examination of the holotype (USNM 20328) revealed that the species belongs to *Pterocirrus* (Fig. 6D–G) and that the animals taken in Belize are conspecific. The holotype is 25.3 mm long, about 3 mm wide without setae, and has 116 setigers (complete apart from anal cirri). The neuropodia have shriveled somewhat and are now brittle (Fig. 6D), and most appendages have been lost, only one tentacular cirrus (Fig. 6E), one dorsal cirrus, and a few ventral cirri remaining. In all points where a comparison was possible, the holotype agreed with the description given above. The pigmentation pattern was identical, although darker on the holotype, possibly the result of prolonged preservation in alcohol.

Pterocirrus foliosus closely resembles *P. macroceros* (Grube, 1860), described from the Adriatic Sea, but differs in having darker pigmentation, much less elongate proboscideal papillae, less elongate dorsal cirri, and more rounded ventral cirri. The latter species has been reported from North Carolina (Gardiner 1975:109, fig. 6k, l) and the Gulf of Mexico (Gathof 1984:19-16, fig. 19-12).

Imajima & Hartman (1964:70) erected the variety *orientalis* of *Pterocirrus macroceros* (as *Sige macroceros*) for animals from Japan having setae beginning on segment 3. According to Imajima & Hartman, European animals have setae beginning on segment 2, whereas they actually begin on segment 4 (pers. obs.) as in *P. foliosus.* This confusion stems from Bergström (1914:98), who synonymized *Sige fusigera* Malmgren, 1865 with *P. macroceros* under the name of *Sige macroceros* (see Eibye-Jacobsen 1987, Pleijel 1990). Fauchald (1977:16) reported (with doubt) a single specimen of Imajima & Hartman's variety (as *Sige orientalis*) from the Atlantic side of Panama. Examination of this animal (USNM 61642), as well as six others from the same investigation (USNM 66009), showed that they are *P. foliosus.*

It is uncertain whether species of *Pterocirrus,* such as *P. foliosus* and *P. macroceros,* should be regarded as having segment 1 completely or only partially reduced dorsally. Stereoscopic viewing of SEM photographs of the dorsoposterior prostomial depression did not allow an opinion to be formed as to whether this depression is part of the prostomium itself or a dorsal vestige of segment 1.

There appears to be a greater tendency for pigment to leach from the eyes of preserved specimens of *P. foliosus* than in the other species reported in this paper, although most were treated identically. On such animals the eyes may be overlooked, making identification difficult.

Small individuals of *P. foliosus* may be confused with *Sige belizensis*, especially if the ventral tentacular cirri of segment 2 have been lost. However, the position of the median antenna, prostomial shape, and neuropodial morphology permit distinction of the two. During quick identification the most obvious difference is that of pigmentation, *P. foliosus* being a much darker species.

Distribution.—Found in Belize in coral rubble (*Acropora palmata, Porites,* and *Agaricia agaricites*), in coral sand, and in bunches of *Halimeda* and *Caulerpa,* at depths of 0–18 m. Needham's Point, Barbados (Treadwell 1924:10, type locality). Galeta Reef, Panama (Fauchald 1977:16).

Genus *Nereiphylla* Blainville, 1828

Nereiphylla mimica, new species

Fig. 7

Material examined.—GH-17.1.76-1 (1); GH-26 (2); GH-32 (2); GH-36 (4); K-35 (1); K-46(1); K-58 (1); K-77 (1); K-107 (1); RC-1 (12); RC-3 (5); RC-8 (4); RC-10 (3); RC-12 (2); RC-18 (1); RC-21 (3); RC-26 (1); RC-34 (3); RC-39 (1); RC-41 (1); RC-52 (1); RC-53 (1); RC-59 (2); RC-60 (1); RC-82 (3); RC-91 (3); RC-92 (2); RC-93 (4); RC-94 (6); RC-96 (2); RC-97 (1); RC-98 (3); RC-100 (4); RC-101 (3); RC-102 (1); RC-103 (1); RC-107 (1); RC-111 (1); RC-112 (1); RC-116 (3); RC-117 (3); RC-118 (7); RC-119 (4); RC-120 (3); F-1 (1); F-45 (2); F-283 (4 paratypes, USNM 144870); DEJ-4 (1 paratype, ZMUC); DEJ-7 (1 paratype, ZMUC); DEJ-9 (1 paratype, ZMUC); DEJ-11 (1 paratype, ZMUC); DEJ-12 (1 paratype, ZMUC); DEJ-14 (1 paratype, ZMUC); DEJ-16 (1 paratype, ZMUC); DEJ-18 (1 paratype, ZMUC); DEJ-21 (holotype + 1 paratype, ZMUC; 3 paratypes, USNM 144871).

Description.—Length up to 4.3 mm (F-283), holotype 2.8 mm long (complete except for anal cirri). Width without setae up to 0.55 mm, holotype 0.45 mm wide. Up to 35 setigers (F-283), 34 on holotype.

Prostomium oval to pentagonal, with straight dorsoposterior margin, broader than long (Fig. 7A); 4 fusiform antennae present, each about as long as prostomium, with dorsal pair inserted just below frontal edge; eyes large, dark red, with lighter red lenses; nuchal papilla absent; nuchal organs not observed.

Proboscis not everted on holotype, observed on 1 specimen only (RC-1); covered with diffusely distributed small rounded papillae; oral papillae not observed.

Tentacular formula 1 + S 1/1 + S 1/N, segment 2 with only 1 or 2 setae on each side. Segment 1 dorsally reduced, ventrally weakly separated from segment 2. Ventral tentacular cirri of segment 2 cirriform, not flattened, reaching to segment 4. Other tentacular cirri of uniform width along most of length, abruptly tapering distally; those of segment 1 reaching to segment 4, dorsal ones of segments 2 and 3 reaching to segment 5 or 6.

All dorsal cirri thick and oval, slightly longer than broad (Fig. 7B). Neuropodial presetal lobe not obviously divided into supra- and sub-acicular lips. Rostrum of setal shaft inflated with distal crown of about 12 teeth (Fig. 7C); distal article of seta short, distally very narrow. All ventral cirri oval, longer than broad, obliquely attached to and as long as or slightly shorter than neuropodium (Fig. 7B). Anal cirri of paratypes oval, distally tapering, about 1½ times as long as broad (Fig. 7D); anal cirri lost on holotype; pygidial papilla absent.

Living animals pale brown with dark brown or rusty brown pigment on antennae,

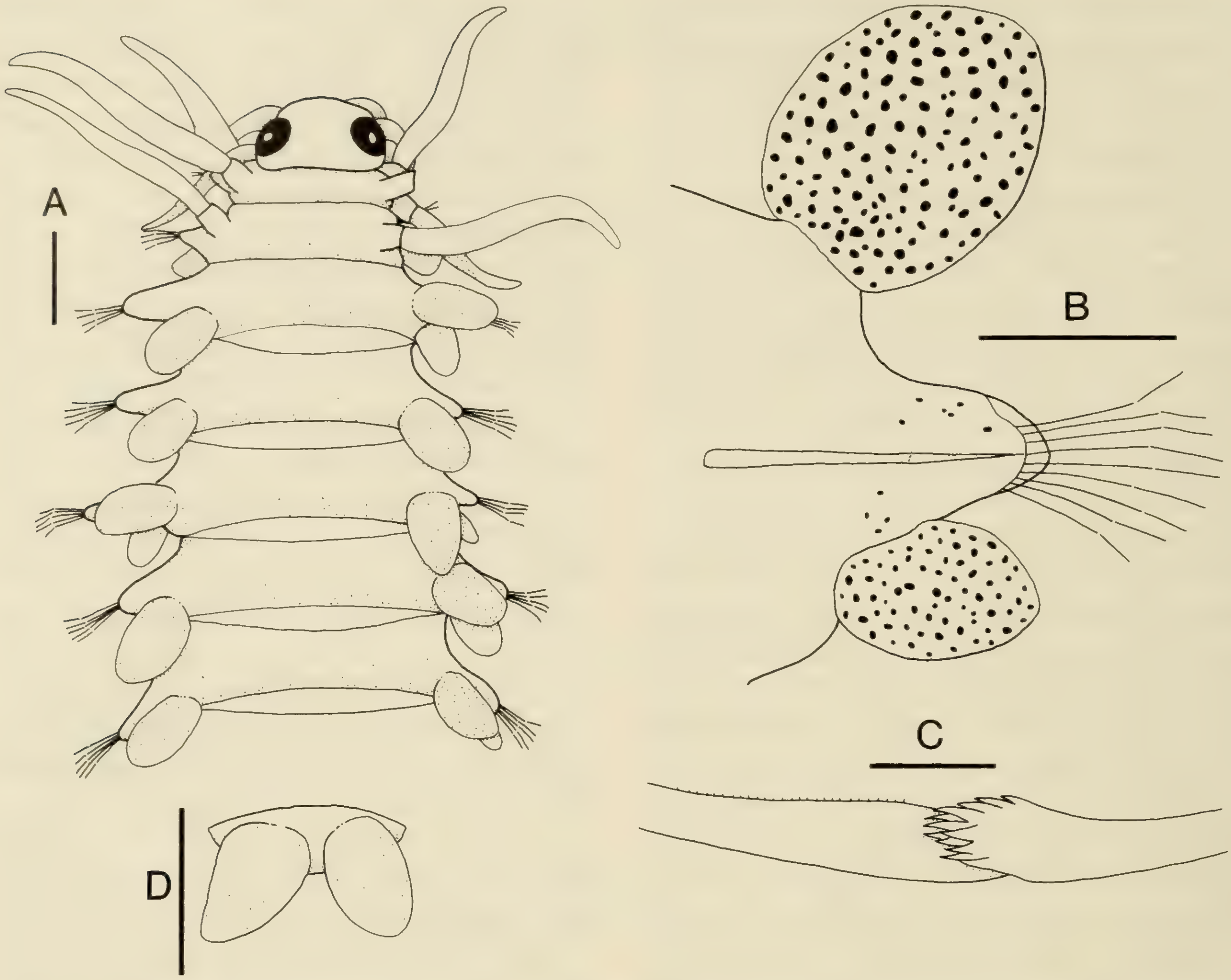

Fig. 7. *Nereiphylla mimica,* new species. A. Anterior end, dorsal view. B. Parapodium of setiger 14, posterior view. C. Seta at region of articulation, from parapodium in B. D. Pygidium with anal cirri, ventral view. A–C: holotype, ZMUC. D: paratype, DEJ-21, ZMUC. Scales: A = 0.1 mm; B = 0.1 mm; C = 10 μm; D = 0.1 mm.

cirri (tentacular, dorsal, ventral, and anal), and anterior prostomium. Pigment reddish brown or dark orange in alcohol, dorsum and venter usually with broad weak transverse band of reddish-brown pigment on each segment; ventral cirri (and occasionally also dorsal ones) may have a few, diffusely distributed red spots in addition to orange or reddish brown color.

No ovigerous females recognized. Material includes 1 male containing sperm (RC-1), 3.3 mm long, with 30 setigers, complete.

Remarks.—Much confusion exists regarding which species of *Nereiphylla* are present in Caribbean and neighboring waters. *Nereiphylla fragilis* (Webster, 1879) and *N. castanea* (Marenzeller, 1879) have both been reported from North Carolina (Gardiner 1975) and the Gulf of Mexico (Hartman 1951, Gathof 1984). A comparison of *N. mimica* with the type material of *N. fragilis* (USNM 535; type locality: Northampton County, Virginia) and *N. castanea* (Naturhistorisches Museum, Vienna 523; type locality: Enosima, Japan) showed that the Belizean animals belong to a distinct species. In addition to their pigmentation, both differ from *N. mimica* in being much bigger and having cordiform dorsal cirri larger relative to the neuropodia and attached to strongly developed cirrophores. Furthermore, *N. castanea* differs from *N. fragilis* and *N. mimica* in having the dorsal tentacular cirri of segments two and three very obviously flattened.

Treadwell (1901) described *Phyllodoce*

magnaoculata from Puerto Rico on the basis of a single specimen. Study of the holotype (USNM 15951), although in very poor condition, revealed that the species belongs to *Nereiphylla.* It differs from *N. mimica* in having reniform dorsal cirri with strongly development cirrophores and is apparently also distinct from *N. fragilis* and *N. castanea.* More material is necessary before this species can be adequately characterized.

Gathof (1984) described some specimens from the Gulf of Mexico as *Genetyllis* sp. A. An examination of some of this material (1 specimen each from USNM 89979, 89980, and 112306) demonstrated that they belong to a species of *Nereiphylla* separate from all those mentioned above. They differ from *N. mimica* in having a triangular to cordiform prostomium, smaller eyes, subulate tentacular cirri, and triangular to oval dorsal cirri. Their pattern of pigmentation is reminiscent of that in *N. mimica,* although it is darker and red spots are lacking on the podial cirri of all specimens.

It is quite easy to confuse living animals of *N. mimica* with *Eumida muriatica,* especially in cases where the median antenna of the latter has been lost. This is due to their almost identical sizes and body proportions, generally pale bodies with darker markings on the dorsal and ventral cirri, and relatively large eyes. Furthermore, as mentioned above, some specimens of *Nereiphylla mimica* also have red spots on the ventral cirri. However, in *E. muriatica* these spots are relatively large and arranged in a line along the ventral border of the cirrus, whereas they are smaller and diffusely distributed on the entire surface in *N. mimica.* The dorsum is pale brown or orange in the latter, yellowish green in the former. Another distinction, useful when working with live animals, is the very different morphologies of their tentacular cirri.

Etymology.—This species is named for its striking, albeit superficial, resemblance to *Eumida muriatica,* new species (mimicus is Latin for imitative, deceptive, acting as, or having the traits of).

Distribution.—Found among epifauna and *Halimeda,* in coral rubble (*Porites, Acropora palmata,* and *A. cervicornis*), and among *Dictyota* on sand and *Caulerpa* in mangroves, at depths of 0–28 m. Known only from Belize (around Carrie Bow Cay, South Water Cay, Tobacco Cay, the Cocoas, and the Sand Bores). Type locality: among epifauna and *Halimeda* on pier, 25 m west of Carrie Bow Cay, Belize, 1 m.

Notes on Other Species

This section is included in order to provide a point of reference for future studies on the phyllodocid fauna of Belize. At present, little more may be said than that these species are present and distinct from those treated above. In addition to the following material, 39 phyllodocid specimens from a total of 33 stations were indeterminable, being either juveniles or in very poor condition.

Phyllodoce sp. A.—A single specimen from st. JDF-20-1 is unusual in having dorsal cirri on middle segments which are very broad, almost reniform. The animal is large, about 95 mm long, and in good condition, but the proboscis is not everted.

Phyllodoce sp. B.—Material examined: K-37(2); K-77 (1); K-102 (2); F-36 (1); F-221 (2). These animals differ from *P. erythrophylla* in having papillae diffusely distributed on the proximal part of the proboscis. They were compared to the type material of *P. panamensis* Treadwell, 1917 (USNM 16831; type locality: Chame Point, Panama, Pacific Ocean) and *P. nicoyensis* Treadwell, 1928 (USNM 19244 + 2 paratypes in USNM 19245; type locality: Gulf of Nicoya, Costa Rica, Pacific Ocean). *P. panamensis* may easily be distinguished by the extreme development of the cirrophores of its dorsal cirri and by having proboscideal papillae in twelve rows with up to 20 papillae in each. *P. nicoyensis* has diffusely distributed papillae on the proboscis, but is unlike Belizean animals in having almost oval dorsal cirri and very pointed ventral cirri. The eight specimens reported here may in fact belong to two species.

Phyllodoce sp. C.—A single specimen from st. K-37 is remarkable in lacking true eyes, although a few spots of pigment may be seen on the prostomium. The proboscis is everted and shows 12 basal rows of up to 8 papillae.

?*Protomystides* sp.—A single specimen of this species was taken at st. DEJ-1. It is complete with about 80 segments, 3.5 mm long, and 0.30 mm wide excluding setae. The prostomium is elongate conical, appears to bear only 4 antennae and has 2 small red eyes. The tentacular formula is 1 + 0? 1/1 + S 1/N, but the ventral tentacular cirri of segment 2 are very short. All segments are fully developed. Dorsal and ventral cirri are oval, the anal cirri have been lost, and the pygidium bears a very long pygidial papilla (about 40 μm long). The animal was golden yellow in life, now yellowish with reddish brown pigment specks on the dorsum as well as the dorsal and ventral cirri.

Eulalia sp.—Only 1 specimen, taken at st. K-102. It is about 10 mm long and brown with dark brown podial cirri. The animal is in poor condition, but appears to belong to the group of species that resemble *E. bilineata* (Johnston, 1865).

Pterocirrus cf. *macroceros* (Grube, 1860).—Material examined: JDF-63-1 (1); RC-70 (1). These animals differ from *P. foliosus* (treated above) in having dorsal cirri which are extremely elongate, up to about 3 times as long as broad. The eyes are very large, with prominent lenses. The dorsum is dark brown, especially on anterior segments, whereas the dorsal cirri are lighter.

Nereiphylla cf. *fragilis* (Webster, 1879).—Material examined: GH-18 (1); K-101 (1). These animals are 3 and 8 mm long respectively and differ from *N. mimica*, new species, in having more elongate and asymmetrical dorsal cirri. It is further distinguished by its uniform dark brown color.

Nereiphylla sp.—A single specimen from st. JDF-13-7 differs from *N. mimica* and *N.* cf. *fragilis* in having very large dorsal cirri and ventral cirri which are almost vertically attached to the neuropodium. The animal is about 25 mm long and is orange-brown with darker cirri.

Together with the species treated in detail above and *Phyllodoce panamensis* Treadwell, 1917 (reported by Young & Young 1982), this brings the total number of phyllodocid species known to be present in Belize to at least 17.

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Appendix: Station Data

In the following, CBC refers to Carrie Bow Cay.

1. Collected by Klaus Ruetzler (material in USNM):

R-23.4.74: 16°48′N, 88°05′W, 0 m, 23 Apr 1974.
R-2.5.74-2: as preceding, rock sample, 1 m, 2 May 1974.
R-4.5.74-3: as preceding, 0.5 m, 4 May 1974.

2. Collected by Joan D. Ferraris at CBC (material in USNM):

JDF-13-7: patch reef, SW of CBC, 2–3 m, 24 Apr 1975.
JDF-15-3: N end of back reef, rubble, 1.5 m, 25 Apr 1975.
JDF-20-1: back reef, *Porites asteroides,* 28 Apr 1975.
JDF-23-2: lagoon, 185 m W of dock, 2–3 m, 29 Apr 1975.
JDF-47-2: transect 520 m, far reef slope, *Agaricia agaricites* slab, 17 m, 14 May 1975.
JDF-63-1: sand trough, rubble, 8 m, 22 May 1975.

3. Collected by Gordon Hendler (material in USNM):

GH-17.1.76-1: rock pile, 17 Jan 1976.
GH-3: 16°42.5′N, 87°51.8′W, Glovers Reef, inner SW Cays, 0–2 m, 23 Mar 1980.
GH-6: 16°45.5′N, 87°52.8′W, Glovers Reef, SW Cays, 0–3 m, 24 Mar 1980.
GH-11: 16°48.2′N, 88°04.5′W, forereef slope, 27.4 m, 26 Mar 1980.
GH-16: as preceding, forereef crest, 15.2 m, 27 Mar 1980.
GH-18: 16°48.9′N, 88°05.9′W, cut at S end of Twin Cays, mangrove, 1–2 m, 28 Mar 1980.
GH-22: 16°48.2′N, 88°04.5′W, 36 m, 29 Mar 1980.
GH-26: 16°48.2′N, 88°04.6′W, 3–6 m, 31 Mar 1980.
GH-32: 16°48.2′N, 88°04.5′W, 15 m, 2 Apr 1980.
GH-36: 16°48.1′N, 88°04.8′W, 0–2 m, 3 Apr 1980.
GH-38: 16°48.2′N, 88°04.6′W, 3–9 m, 4 Apr 1980.

4. Collected by Anne Cohen at CBC (material in USNM):

AC-509: spur and groove, sand and rubble, 8.4 m, 26 Oct 1979, coll: A. Cohen.
AC-520: transect, sand trough next to outer reef edge, 23 m, 31 Oct 1979, coll: A. Cohen & Rath.

5. Collected by Brian Kensley (at CBC unless otherwise noted; material in USNM):

K-33: rubble and pavement, mainly *Acropora* rubble, 1 m, 5 Apr 1979.
K-35: center slope of reef, rubble, few *Thalassia* clumps, 18 m, 5 Apr 1979.
K-36: as preceding, rubble with attached algae and sponges, 10–18 m.
K-37: sand trough on outer reef slope, coarse sediment and small rubble, 25 m, 6 Apr 1979.
K-43: *Porites* rubble in flats behind spur and groove area, 1 m, 8 Apr 1979.
K-46: Twin Cays?, *Caulerpa verticillata* carpet under dense mangrove shade, 0.1–0.2 m, 9 Apr 1979.
K-47: lagoon, in *Padina* clumps growing on coral rubble, 1 m, 10 Apr 1979.
K-49: spur and groove, rubble, 8–9 m, 10 Apr 1979.
K-53: *Dictyota dichotoma* clumps growing on rubble, coarse sandy sediment, 1 m, 12 Apr 1979.
K-55: reef crest E of CBC, clumps of *Caulerpa racemosa* with attached rubble, 0.1–0.3 m, 15 Apr 1979.
K-58: sand and rubble zone, back reef rubble, 4 m, 28 Oct 1979.
K-60T: rubble and pavement, *Halimeda* from back reef, 1–2 m, 29 Oct 1979.
K-62b: 2 km SW of CBC, rubble and coarse sediment from bare patches in algal mat, 5–8 m, 30 Oct 1979.
K-64: buttress base, upper spur and groove, coral rubble, 5–8 m, 1 Nov 1979.
K-66: lagoon E of CBC, *Amphiroa* clumps between *Thalassia,* 0.2 m, 3 Nov 1979.
K-70b: E of CBC, sand trough on reef, *Dictyota* on rubble, 28 m, 6 Nov 1979.
K-70c: as preceding, rubble lying in pockets.
K-74: outer reef ridge, pockets of rubble, 15 m, 12 Nov 1979.
K-77: sand trough, coarse rubble and sediment, scattered *Dictyota,* 28 m, 12 Mar 1980.
K-96: coarse sediment and coral fragments, scattered gorgonians, 6 m, 7 Apr 1981.
K-98: reef crest, rubble with encrusting corallines and algal turf, 0.1–0.2 m, 10 Apr 1981.
K-101: edge of sand trough near drop-off, rubble, 25 m, 14 Apr 1981.
K-102: outer edge of outer ridge, rubble, 22 m, 9 Jun 1981; coll: B. Kensley & P. Hutchings.
K-107: South Water Cay, intertidal rocky platform, coral rubble with orange-brown encrusting alga, 0.3 m, 13 Jun 1981.

6. Collected on the reef crest east of CBC as part of the Reef Crest Survey Project of USNM (all material collected by Brian Kensley and Kristian Fauchald; material in USNM):

RC-1 to RC-5: coral rubble with *Homotrema* and *Lithothamnion,* from between *Thalassia,* 0.2–0.3 m, 5 Nov 1979.
RC-6 to RC-10: as preceding, 6 Nov 1979.
RC-11 to RC-15: coral pavement and *Lithothamnion,* 0.3 m, 6 Nov 1979.
RC-16 to RC-20: coral rubble, 0.2–0.3 m, 8 Nov 1979.
RC-21 to RC-25: coral rubble, upper layer covered with algal turf, 0.1–0.2 m, 9 Nov 1979.
RC-26 to RC-30: on highest part of reef crest, coral pavement and algal turf, 10 Nov 1979.
RC-31 to RC-35: rubble between *Thalassia,* 4 Mar 1980.

RC-36 to RC-40: as preceding, 5 Mar 1980.
RC-41 to RC-45: rubble with algal carpet, 7 Mar 1980.
RC-46 to RC-50: as preceding, 9 Mar 1980.
RC-51 to RC-55: rubble without vegetation, 10 Mar 1980.
RC-56 to RC-60: as preceding, 12 Mar 1980.
RC-61 to RC-65: as preceding, 14 Aug 1980.
RC-66 to RC-75: rubble with algal turf, 15 Aug 1980.
RC-76 to RC-80: rubble without vegetation, 15 Aug 1980.
RC-81 to RC-90: rubble between *Thalassia,* 16 Aug 1980.
RC-91 to RC-95: as preceding, 3 Dec 1980.
RC-96 to RC-100: as preceding, 4 Dec 1980.
RC-101 to RC-105: rubble with algal turf, 6 Dec 1980.
RC-106 to RC-110: as preceding, 7 Dec 1980.
RC-111 to RC-115: rubble without vegetation, 9 Dec 1980.
RC-116 to RC-120: as preceding, 10 Dec 1980.

7. Collected by Kristian Fauchald unless otherwise noted (material in USNM):

F-1: S of CBC, inside edge of reef, old coral blocks, 0.3 m, 4 Apr 1979.
F-4: SE of CBC, rubble field, *Acorpora* rubble, 0.25 m, 8 Apr 1979.
F-21: E of CBC, 3 m inside edge of turtlegrass, coral sand, 0.3 m, 28 Oct 1979.
F-25: 10 m from inner end of transect at CBC, coral rubble and *Dictyota,* 1.2 m, 1 Nov 1979.
F-27: 10 m N of CBC, *Thalassia* bed, coral rubble and sand, 0.4 m, 4 Nov 1979.
F-30: 10 m E of CBC, shallow rubble field on reef flat, *Porites* rubble, 0.3 m, 5 Nov 1979.
F-35: 90 m SW of CBC, *Thalassia* bed, coral rubble, 0.7 m, 8 Nov 1979.
F-36: SW of CBC, *Thalassia* bed, sand, 0.6 m, 9 Nov 1979.
F-39: 10 m NW of CBC, sand field near *Dictyota,* 0.6 m, 10 Nov 1979.
F-41: 20–25 m SW of CBC, near edge of *Thalassia* bed, sand, 11 Nov 1979.
F-42: 6 m NW of CBC, at base of *Dictyota* covered block, sand, 0.3 m, 12 Nov 1979.
F-44: 10 m SW of CBC, coral rubble, 0.3 m, 12 Nov 1979.
F-45: 25 m SW of CBC, coral rubble, 0.6 m, 12 Nov 1979.
F-48: 20 m S of CBC, well-encrusteed coral rubble, 0.7 m, 13 Nov 1979.
F-65: 100–200 m N of CBC, sand, sparse *Thalassia,* rubble, 1 m, 15 Aug 1980.
F-116: 15–20 m W of CBC, rubble field, *Thalassia,* fist-sized rubble, 0.4 m, 11 Dec 1980.
F-135: SW of CBC, rubble field, rubble, 0.25 m, 9 Apr 1981.
F-147: as preceding, old rubble, 0.1 m, 13 Jun 1981.
F-221: channel NW of CBC, inside reef flat, *Thalassia* on sand, rubble, 36 m, 19 Nov 1983.
F-261: about 30 m S of CBC, reef flat, rubble of branching *Acropora,* 0.6 m, 26 Oct 1988.
F-263: N side of CBC, near old transect, *Porites* rubble, rounded and full of holes, 0.2 m, 26 Oct 1988, coll: K. Fauchald & L. Ward.
F-265: E of CBC, at reef edge, *Agaricia* rubble, 12 m, 27 Oct 1988, coll: B. Littman & M. Carpenter.
F-266: 100 m E of CBC, reef crest, rubble and algal turf with *Halimeda,* 1 m, 28 Oct 1988, coll: K. Fauchald & L. Ward.
F-269: E of CBC, upper spur and groove of reef crest, rubble sample, 10 m, 29 Oct 1988, coll: B. Littman.
F-270: E of CBC, inside reef crest, upper end of dead *Acropora palmata* type of coral, 0.2 m, 31 Oct 1988.
F-274: NE end of Blue Ground range, N Cocoas, rubble of *Acropora palmata,* 0.6 m, 1 Nov 1988, coll: K. Fauchald & D. Eibye-Jacobsen.
F-275: E of CBC, spur and groove of reef crest, rubble and sand, 8 m, 2 Nov 1988, coll: B. Littman.
F-278: Columbus Reef, N of Tobacco Cay, in shallows about 30 m from reef crest, rubble sample, 1 m, 3 Nov 1988, coll: M. Carpenter & L. Ward.
F-279: as preceding, inside outer reef crest, rubble sample, 0.6 m.
F-281: SW of CBC, S of boat ramp, sand and *Thalassia* bottom, in bunches of *Halimeda,* 1 m, 5 Nov 1988, coll: K. Fauchald & L. Ward.
F-282: N of South Water Cay, sand and rubble flats about 100 m from reef crest, rubble sample, 1 m, 6 Nov 1988, coll: L. Ward.
F-283: 10 m SW of CBC, S of boat ramp, bunches of *Halimeda,* 1 m, 7 Nov 1988, coll: L. Ward.
F-285: E of CBC, spur and groove, rubble sample, 15 m, 7 Nov 1988, coll: B. Littman.

8. Collected by or for the author (material in ZMUC unless otherwise noted in text):

DEJ-1: 600 m E of CBC, spur and groove, poorly sorted sand and *Halimeda* gravel, 12 m, 27 Oct 1988, coll: J. Norenburg, B. Littman & M. Carpenter.
DEJ-2: 600 m E of CBC, at reef edge, dead *Agaricia,* 12 m, 27 Oct 1988, coll: J. Norenburg, B. Littman & M. Carpenter.
DEJ-3: 50 m N of CBC, lagoon, dead *Porites,* 0.5 m, 28 Oct 1988, coll: K. Fauchald.
DEJ-4: 50 m N of CBC, lagoon, dead *Porites,* 0.5 m, 28 Oct 1988, coll: D. Eibye-Jacobsen. (Type locality of *Eumida muriatica,* new species)
DEJ-5: 500 m E of CBC, spur and groove, rubble and well-sorted sand, 9 m, 29 Oct 1988, coll: B. Littman.
DEJ-6: 100 m E of CBC, lagoon just behind reef

crest, dead *Acropora palmata,* 0.5 m, 31 Oct 1988, coll: K. Fauchald.

DEJ-7: 75 m N of CBC, lagoon, dead *Porites,* 0.5 m, 1 Nov 1988, coll: D. Eibye-Jacobsen.

DEJ-8: 250 m S of CBC, S channel, medium fine, well-sorted sand, 4.5 m, 2 Nov 1988, coll: J. Norenburg, B. Littman & M. Carpenter.

DEJ-9: 200 m NE of CBC, outer edge of reef crest, dead *Acropora palmata,* 0.5 m, 2 Nov 1988, coll: V. Solis-Weiss.

DEJ-10: 400 m E of CBC, spur and groove, dead *Agaricia* and sand, 8 m, 2 Nov 1988, coll: B. Littman.

DEJ-11: Cocoas, E of Blue Ground Range, dead *Acropora palmata,* 0.5 m, 3 Nov 1988, coll: K. Fauchald & L. Ward.

DEJ-12: N of Tobacco Cay, W of S end of Columbus Reef, just behind reef crest, dead *Porites,* 0.5 m, 3 Nov 1988, coll: D. Eibye-Jacobsen.

DEJ-13: as preceding, dead *Acropora palmata,* 0.6 m, coll: K. Fauchald.

DEJ-14: 50 m S of CBC, lagoon, dead *Porites,* 0.3 m, 4 Nov 1988, coll: D. Eibye-Jacobsen. (Type locality of *Sige belizensis,* new species)

DEJ-15: 200 m E of CBC, spur and groove, medium-fine, poorly sorted sand, 4.5 m, 4 Nov 1988, coll: J. Norenburg, B. Littman & M. Carpenter.

DEJ-16: SW of CBC, S of boat ramp, sand bottom with *Thalassia,* in bunches of *Halimeda,* 1 m, 5 Nov 1988, coll: K. Fauchald & L. Ward.

DEJ-17: N of Sand Bores, E of Blue Ground Range, dead *Acropora cervicornis,* 2 m, 5 Nov 1988, coll: D. Eibye-Jacobsen.

DEJ-18: 150 m N of South Water Cay, just behind reef crest, dead *Porites,* 0.2 m, 6 Nov 1988, coll: D. Eibye-Jacobsen.

DEJ-19: 600 m SE of CBC, spur and groove, fine sand with silt, 16 m, 7 Nov 1988, coll: J. Norenburg, B. Littman & M. Carpenter.

DEJ-20: as preceding, dead *Acropora palmata,* coll: B. Littman.

DEJ-21: 25 m W of CBC, scrapings from pier, sponges, tunicates, empty barnacles, *Halimeda,* 1 m, 7 Nov 1988, coll: D. Eibye-Jacobsen. (Type locality of *Nereiphylla mimica,* new species)

DEJ-22: 200 m NE of CBC, spur and groove, sand, 8 m, 8 Nov 1988, coll: J. Norenburg, B. Littman & M. Carpenter.

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TWO NEW GENERA AND FOUR NEW COMBINATIONS OF SIGALIONIDAE (POLYCHAETA)

Marian M. Pettibone

Abstract.—Among the heterogeneous group of sigalionid species originally assigned to *Leanira* Kinberg, 4 species are separated and referred to new genera: *Labioleanira* and *Labiosthenolepis,* both genera each with two new combinations, and there is also one junior synonym in *Labiosthenolepis.* These new genera are characterized by labial lobes on the lateral lips of the ventral mouth.

Of the heterogeneous group of sigalionid species that have spinigerous or distally pointed, camerated or canaliculate compound neurosetae, four genera have been treated previously by me: *Leanira* Kinberg, 1856, limited by Pettibone, 1970b: *Ehlersileanira* Pettibone, 1970b:19; *Neoleanira* Pettibone, 1970c:367; and *Horstileanira* Pettibone, 1970c:377. Willey estabished the genus *Sthenolepis* for four species of *Leanira* described by McIntosh (1885) from the *Challenger* Expedition, including *L. areolata* and *L. japonica,* both from Japan, *L. laevis,* from New Zealand, and *L. magellanica,* from the Magellan area. *L. japonica* was designated as the type species of *Sthenolepis* by Hartman (1965:54). *L. areolata* and *L. magellanica* were referred to *Neoleanira* by Pettibone (1970c). *L. laevis* is herein referred to *Labiosthenolepis,* new genus, along with a second species, *Leanira sibogae* Horst, 1917. Species of *Sthenolepis* will be treated in a subsequent paper. Two additional species of *Leanira* are herein referred to *Labioleanira,* new genus: *L. yhleni* Malmgren, 1867 and *L. tentaculata* Horst, 1917. The new genera are characterized by labial lobes on the lateral lips of the ventral mouth. Some species of *Leanira* also display this character.

In addition to the sigalionid collections in the Smithsonian Institution (USNM), material was obtained on loan or in exchange from the following sources: British Museum (Natural History), London (BMNH), through J. D. George: Museum National d'Histoire Naturelle, Paris (MNHNP), through J. Renaud-Mornant; Naturhistoriska Riksmuseet, Stockholm (NRS), through R. Oleröd; Queensland Museum, Brisbane (QMB), through B. Campbell; Rijksmuseum van Natuurlijke Historie, Leiden (RNHL), through J. van der Land; Zoölogisch Museum Universiteit van Amsterdam (ZMA), through S. van der Spoel; Zoologisches Museum, Berlin (ZMB), through G. Hartwich; Zoologisches Staatsmuseum, Hamburg (ZMH), through G. Hartmann-Schröder. Additional material was received from Australia via H. Paxton; from Tonga, via J. Bailey-Brock; and from the Tyrrhenian Sea via M. C. Gambi. The manuscript benefited from the suggestions of Pat Hutchings and two anonymous reviewers.

Labiosthenolepis, new genus

Type species.—*Leanira laevis* McIntosh, 1885. Gender, feminine. For *Labiosthenolepis laevis* (McIntosh, 1885), new combination, with synonym *Sthenelais semitecta* Ehlers, 1905, and *Labiosthenolepis sibogae* (Horst, 1917), new combination (as *Leanira*).

Diagnosis.—Body elongate, with numerous segments (up to 130), flattened dorsoventrally, tapering posteriorly. Elytra and elytrophores on segments 2, 4, 5, 7, continuing on alternate segments to 27, then on every subsequent segment; elytra delicate, smooth, without papillae or tubercles; dorsal tubercles on some non-elytrigerous segments; cirriform branchiae attached to elytrophores and dorsal tubercles; parapodial ctenidia, 3 per parapodium, located dorsally to notopodium. Prostomium oval, fused to tentacular segment (I), with 3 antennae: ceratophore of median antenna long, stout, with lateral auricles and long style; lateral antennae small, attached to inner dorsal side of I; 2 pairs of eyes; paired palps long, tapering, emerging ventral to tentacular parapodia, with longer inner and shorter outer palpal sheaths; tentaculophores with long dorsal and short ventral tentacular cirri, with L-shaped inner tentacular lobe; setal lobe with single aciculum and well-developed bundle of capillary setae, directed anteriorly. Buccal segment (II) with first pair of elytra and elytrophores, biramous parapodia with stylodes; ventral buccal cirri larger than following ventral cirri; lateral lips of ventral mouth with flattened or lobulate labial lobes. Segment III without dorsal cirri, with or without small dorsal tubercles. Parapodia biramous, notopodia with subdistal bract with circlet of stylodes and large distal stylode; neuropodia with presetal conical acicular lobe and bilobed postsetal lobe, both with stylodes; notosetae long, capillary, smooth and spinose; neurosetae compound spinigers, with blades canaliculate, tapering to fine tips; without additional simple neurosetae. Ventral cirri short, tapered, with rounded knob on base. Pharynx with 11 pairs of border papillae and 2 pairs of jaws. Pygidium with pair of long anal cirri.

Remarks.—*Labiosthenolepis* agrees with *Sthenolepis* Willey, 1905, *Neoleanira* Pettibone, 1970c, and *Horstileanira* Pettibone, 1970c, in having inner tentacular lobes on segment I and the ceratophore of the median antenna with lateral auricles. *Neoleanira* differs in having long dorsal cirri on segment III, lacking in the other three genera, and rather long lateral antennae attached to the tentaculophores of segment I, instead of small, inconspicuous lateral antennae. Dorsal tubercles are present on segment III on *Horstileanira* and *Sthenolepis,* and small or lacking on *Labiosthenolepis.* The neuropodia of *Horstileanira* have four parapodial bracts, two presetal and two postsetal; the neuropodia of *Sthenolepis* and *Labiosthenolepis* have conical presetal acicular lobes and bilobed postsetal lobes or bracts. *Labiosthenolepis* differs from the above three genera by the presence of labial lobes on the lateral lips of the ventral mouth.

Etymology.—*Labio,* labium or lip, plus *Sthenolepis,* in reference to the labial lobes on the lateral lips on the ventral mouth and its close relationship to *Sthenolepis.*

Labiosthenolepis laevis (McIntosh, 1885), new combination
Figs. 1, 2

[Not *Leanira laevis* McIntosh, 1874:268. *Nomen nudum.*]

Leanira laevis McIntosh, 1885:156, pl. 20: fig. 4, pl. 23: figs. 10, 11, pl. 14A: fig. 3.—Knox, 1960:95.

Sthenelais semitecta Ehlers, 1905:10, pl. 1: figs. 10–12, pl. 2: figs. 1–4.—Benham, 1909:2.

Sthenolepis laevis.—Augener, 1924:271.—Hartman, 1965:14 (Catalogue).—Day and Hutchings, 1979:93.

Material examined.—South Pacific Ocean: Queen Charlotte Sound, New Zealand, 18 m, *Challenger* sta, holotype of *Leanira laevis* (BMNH 1885.12.1.119b). Lyttelton, New Zealand, M. Suter, coll., 1897, 100+ syntypes of *Sthenelais semitecta* (ZMH 3224, 5398; ZMB 6720; USNM 55111).

Remarks.—The name *Leanira laevis* was first used by McIntosh (1874: 268) for some specimens collected by the *Porcupine* Expedition in 1869 but without describing the animals. Later, in the more detailed report on the *Porcupine* polychaetes, McIntosh

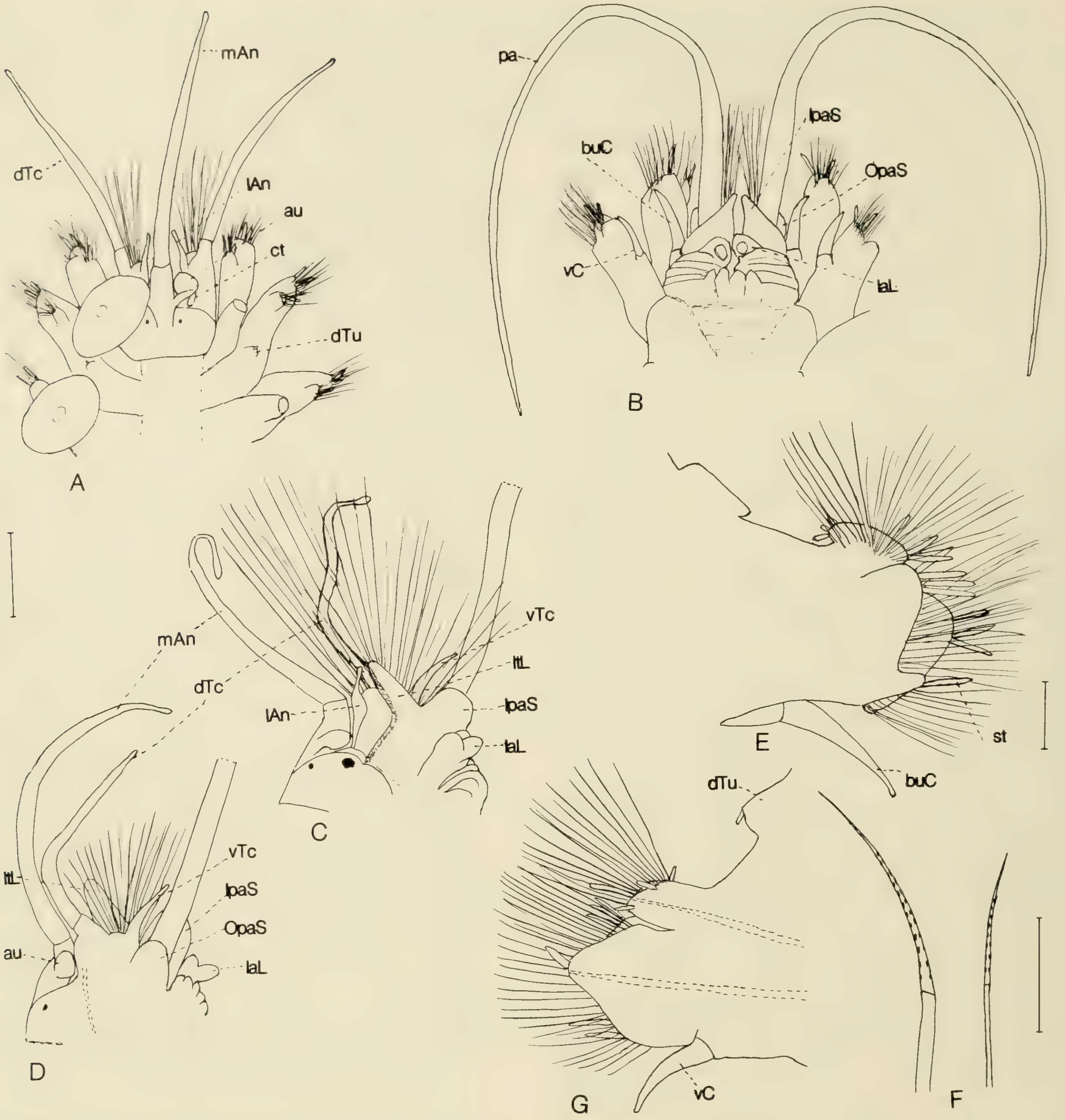

Fig. 1. *Labiosthenolepis laevis,* syntypes of *Sthenelais semitecta* (ZMB 6720): A, Dorsal view of anterior end, palps not shown; B, Ventral view of anterior end; C, Lateral view of prostomium and inner view of left I (right I removed), left palp partially shown: D, Lateral view of prostomium and outer view of right I, aciculum dotted, right palp partially shown; E, Right elytrigerous parapodium of segment II, posterior view; F, Upper and lower neurosetae from same; G, Right parapodium of segment III, anterior view, acicula dotted. Scales = 0.5 mm for A–D; 0.2 mm for E, G; 0.1 mm for F. ac, aciculum; au, auricle or antennal ctenidum; br, branchia; buC, buccal cirri (segment II); ct, ctenidium; dTc, dorsal tentacular cirrus; dTu, dorsal tubercle; elph, elytrophore; IpaS, inner palpal sheath; ItL, inner tentacular lobe; laL, labial lobe on lateral lip (segment II); lAn, lateral antenna; mAn, median antenna; nuO, nuchal organ; OpaS, outer palpal sheath; pa, palp; sp, segmental papilla; st, stylode; vC, ventral cirrus; vTc, ventral tentacular cirrus.

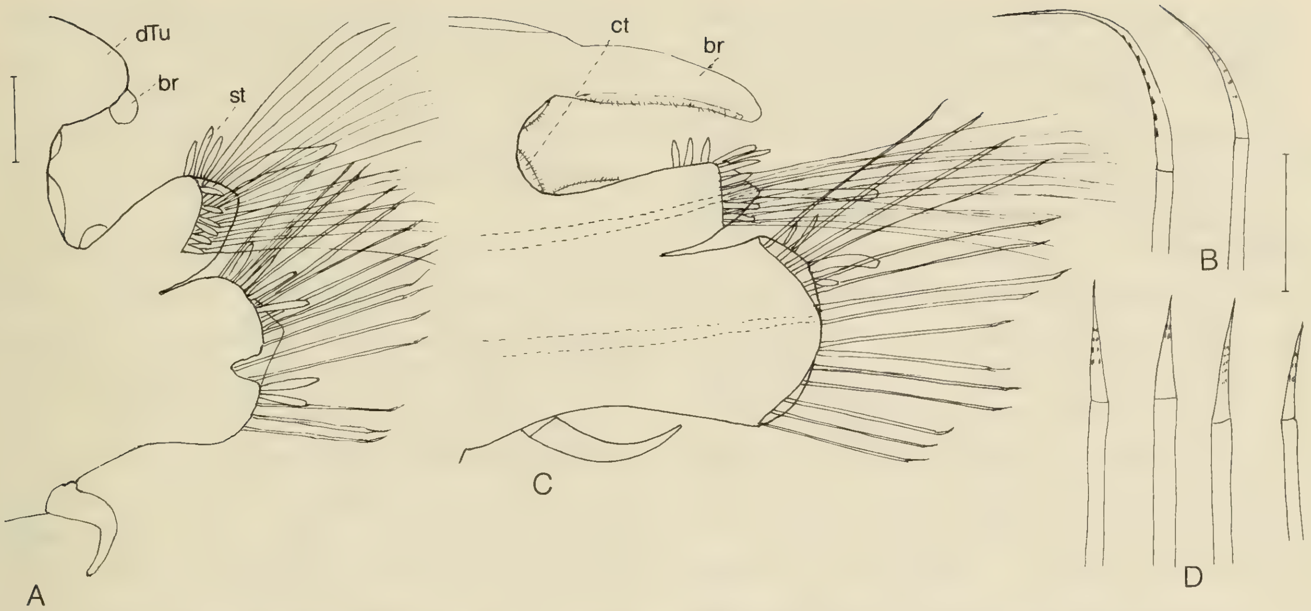

Fig. 2. *Labiosthenolepis laevis,* syntype of *Sthenelais semitecta* (ZMB 6720): A, Anterior parapodium with dorsal tubercle and small branchia, posterior view; B, Lower and upper neurosetae from same; C, Middle elytrigerous parapodium, anterior view, acicula dotted; D, Upper, middle and lower neurosetae from same. Scales = 0.2 mm for A,C; 0.1 mm for B, D. For abbreviations, see Fig. 1.

(1876:408) referred these specimens to *Leanira hystricis* Ehlers, 1874. *Leanira laevis* McIntosh (1874) must be considered to be a *Nomen nudum,* as pointed out by Pettibone (1970b:8), and thus *Leanira laevis* McIntosh, 1885 is not a *Homonym,* as indicated by Hartman (1965:14) in her Catalogue, and the name is available for the *Challenger* specimen from New Zealand. *Sthenelais semitecta* Ehlers, 1905, also from New Zealand, was referred to *Sthenolepis laevis* McIntosh, 1885 by Augener (1924: 271). The numerous available syntypes of *S. semitecta* serve to supplement the description of *L. laevis.*

Type material.—The holotype of *Leanira laevis* consists of an anterior fragment (in two pieces) of 29 segments. The more than 100 syntypes of *Sthenelais semitecta* consist mostly of fragments; a complete specimen is 30 mm long, 3.5 mm wide, and 112 segments. An anterior fragment of 36 segments is 18 mm long and 4.5 mm wide. Over 10 percent of the syntypes had parasitic copepods on the prostomia.

Description.—Body elongate, flattened dorsoventrally, largest in anterior third, tapering gradually posteriorly. Elytra oval, overlapping anteroposteriorly, leaving middorsum uncovered (Fig. 1A; McIntosh 1885; pl. 20: fig. 4, pl. 23: fig. 10; Ehlers 1905, pl. 1: fig. 10).

Prostomium and tentacular segment (I) fused basally; prostomium oval, twice as wide as long; ceratophore of median antenna long, stout, with large lateral auricles and long style, enlarged subterminally, with bulbous tip; lateral antennae short, subulate, with clavate tips, fused to dorsal-inner sides of I: posterior pair of eyes small, lateral to base of ceratophore; anterior pair very large, hidden from view dorsally by lateral auricles; palps long, emerging ventral to I, with rounded inner and shorter rounded outer palpal sheaths; tentaculophores each with single aciculum, long dorsal tentacular cirrus, similar to and slightly shorter than median antenna, and much shorter ventral tentacular cirrus; L-shaped inner tentacular lobe, fused basally to inner palpal sheath; radiating bundle of long capillary setae on outer side of I; small dorsal ctenidia on dorsal side of I, lateral to antennal auricles (Fig. 1A–D; Ehlers 1905, pl. 1: figs. 10–12).

Biramous parapodia of segment II or buccal segment with fleshy labial lobes on lateral lips of ventral mouth (Fig. 1B–D); notopodium rounded, with stylodes and radiating bundle of capillary notosetae, smooth and spinose; larger neuropodium with conical presetal acicular lobe with stylodes and shorter bilobed postsetal lobe with stylodes; ventral buccal cirri extending about to tip of neuropodium (Fig. 1E; Ehlers 1905, pl. 2: fig. 1); fan-shaped bundle of neurosetae all compound spinigers, with blades rather long, canaliculate, lower ones more slender (Fig. 1F). Parapodium of segment III similar to II, but with shorter ventral cirrus; small dorsal tubercle with distal papilla (Fig. 1G).

More posterior parapodia with branchiae beginning about segment 6, attached to dorsal tubercles or elytrophores, small at first, becoming longer, digitiform more posteriorly; parapodial ctenidia, 3 per parapodium, dorsal to notopodium, also beginning about segment 6 (Fig. 2A, C). Notopodium with circlet of stylodes on subdistal bract and extra long distal stylode; neuropodium with scattered distal stylodes; short ventral cirrus with basal knob (Fig. 2A, C; Ehlers 1905, pl. 2: figs. 2–4). Neurosetae with canaliculate spinigerous blades, becoming shorter in more posterior parapodia (Fig. 2B, D). Pharnyx with 11 dorsal and 11 ventral border papillae and 2 pairs of dark brown jaws. Pygidium with pair of long anal cirri.

Distribution.—South Pacific Ocean, off New Zealand, in 5–549 m.

Labiosthenolepis sibogae (Horst)
Figs. 3, 4

Leanira sibogae Horst, 1917:115, pl. 24: figs. 1–3 (part; not sta 313; not 5 specimens from sta 51).

Leanira japonica.—Monro, 1937:263. Not McIntosh, 1885.

Leanira yhleni.—Rullier, 1965:171.—Stephenson, Williams, & Lance, 1970:466, 468. Not Malmgren, 1867.

Sthenolepis yhleni.—Day & Hutchings, 1979:93 (record of *L. yhleni* by Rullier, 1965). Not Malmgren, 1867.

Labiosthenolepis sibogae.—Bailey-Brock, 1984:62A (Abstract); 1987:293, Appendix (in litt. from M. Pettibone).

Remarks.—Fauvel (1932:33) and Uschakov and Wu (1959:37) referred *L. sibogae* Horst (1917) to *L. japonica* McIntosh (1855). Based on a re-examination of the type-specimens, the two species are herein considered to be distinct.

Material examined.—Malay Archipelago, *Siboga* stations: Anchorage off Djangkar, Java, 07°42′5, 114°12.5′E, 9 m, coarse sand, sta 4, 9 Mar 1899, 6 syntypes (ZMA 526.1; RMHL 1168; USMM 55115). Bay of Labuan Tring, west coast Lombok. 08°44.5′S, 116°02.5′E, 18–27 m, mud, coral sand, sta 19, 21 Mar 1899, 2 syntypes (ZMA 526.2; RNML 1167). Bay of Bima, 55 m, mud, fine coral sand, sta 47, 8 Apr 1899, syntype (ZMA 526.3). Molo Strait, 69–91 m, fine grey sand, coarse sand with shells and stones, sta 51, 19 Apr 1899, 2 syntypes (ZMA 526.4; RNML 1166). Saleyer Anchorage, up to 36 m, mud and sand, sta 213, 26 Oct 1899, 4 syntypes (ZMA 526.5, 526.7).

Maldives, the John Murray Expedition, sta 137, 142B, 23, 30 Mar 1934, 37–46 m, 5 specimens (BMNH 1937.9.2.64–67, by Monro, 1937, as *L. japonica*).

Australia, Moreton Bay, S.E. Queensland, ¾ mi S.W. M3 Red Beacon, 10 Nov 1961, W. S. Stephenson, collector, 3 specimens (QMB G3971, as *L. yhleni* by Stephenson et al. 1970); 2 mi E. Woody Point Light, 7 m, mud, 15 Dec 1964, 3 specimens (QMB G4830; USMM 55113, as *L. yhleni* by Rullier 1965). Queensland, Halifax Bay, north of Townsville, 19°09′S, 146°37′E, 5 m, Jan 1977, H. Paxton, collector, 1 specimen (USNM 69376).

Tonga, Tapu Lagoon, 0–6 m, among *Halimeda,* soft mud, 23/24 Sep 1981, R. Brock, collector, 4 specimens (USMM 74412-4).

Type material.—Of the 19 syntypes of *Leanira sibogae* examined (ZMA, RMHL, USNM), 4 syntypes from sta 51 were referred by me to *Sthenelais* sp. and the syntype from sta 313 was made the holotype of *Horstileanira vanderspoeli* by Pettibone (1970c:378). The largest of the 14 remaining syntypes consists of about 100 segments, 50 mm long and 4 mm wide.

Description.—Elytra oval, delicate, without papillae or tubercles, leaving mid-dorsum uncovered. Prostomium and tentacular segment (I) fused basally; prostomium oval, wider than long; ceratophore of median antenna on anterodorsal side of prostomium, long, stout, with prominent winglike lateral auricles and very long, tapering style; lateral antennae short, fused to dorsal inner sides of I; posterior pair of eyes lateral to base of ceratophore; much larger anterior pair of eyes hidden from view dorsally by lateral auricles; palps very long, emerging ventral to I, with large oval inner palpal sheath and shorter outer palpal sheath; tentaculophores each with single aciculum, long dorsal tentacular cirrus, similar to and slightly shorter than median antenna, and very short ventral tentacular cirrus; L-shaped inner tentacular lobe fused basally to inner palpal sheath: 2 groups of long capillary setae extending anteriorly, upper ones longer, smooth and spinous, lower ones shorter and smooth; dorsal side of I with oval ctenidium and few short stylodes between lateral antenna and base of dorsal tentacular cirrus (Fig. 3A, B; Horst 1917, pl. 24: figs. 1, 3).

Segment II or buccal segment with flattened tongue-like labial lobes on lateral lips of ventral mouth (Fig. 3B); biramous parapodium with notopodium rounded, with circlet of stylodes and radiating bundle of long capillary notosetae, upper ones spinose, lower ones smooth; larger neuropodium with conical presetal acicular lobe with stylodes and shorter bilobed postsetal lobe with stylodes; ventral buccal cirrus extending beyond distal tip of neuropodium (Fig. 3C); fan-shaped bundle of neurosetae all compound spinigers, with blades long, curved, canaliculate, with fine tips (Fig. 3D). Segment III without dorsal cirri or dorsal tubercles (Fig. 3A; Horst 1917, pl. 24: fig. 3); parapodia similar to segment II but with shorter ventral cirri (Fig. 3E).

More posterior parapodia with branchiae beginning about segment 6, attached to dorsal tubercles or elytrophores, small at first, becoming longer, digitiform more posteriorly; parapodial ctenidia, 3 per parapodium, dorsal to notopodia, beginning about segment 12 (Fig. 4A, C). Notopodium with circlet of stylodes on subdistal bract and extra long distal stylode; neuropodium with presetal conical acicular lobe with distal stylodes and bilobed postsetal lobe with upper and lower groups of stylodes; short ventral cirrus with basal knob and articulate tip (Fig. 4A, C; Horst 1917, pl. 24: fig. 3). Neurosetae all compound spinigers with rather long canaliculate blades, lower ones more slender, with shorter blades (Fig. 4B, D).

Distribution.—Indo-Pacific, Malay Archipelago, Maldives, Australia, Tonga, in 0–91 m.

Labioleanira, new genus

Type species.—*Leanira yhleni* Malmgren, 1867. Gender, feminine. For *Labioleanira yhleni* (Malmgren, 1867), new combination and *Labioleanira tentaculata* (Horst, 1917), new combination

Diagnosis.—Body elongate, with numerous segments (up to 140), flattened dorsoventrally, tapering posteriorly. Elytra and elytrophores on segments 2, 4, 5, 7, continuing on alternate segments to 27, then on every segment; elytra delicate, smooth, without papillae or tubercles. Cirriform branchiae attached to elytrophores or dorsal tubercles on non-elytrigerous segments; parapodial ctenidia, 3 per parapodium, dorsal to notopodium. Prostomium oval, fused to tentacular segment (I), with 3 antennae: ceratophore of median antenna stout, with lateral auricles and long style; lateral antennae small, attached to inner dorsal side of segment I; 2 pairs of eyes; paired palps long, tapering, emerging ventral to tentacular

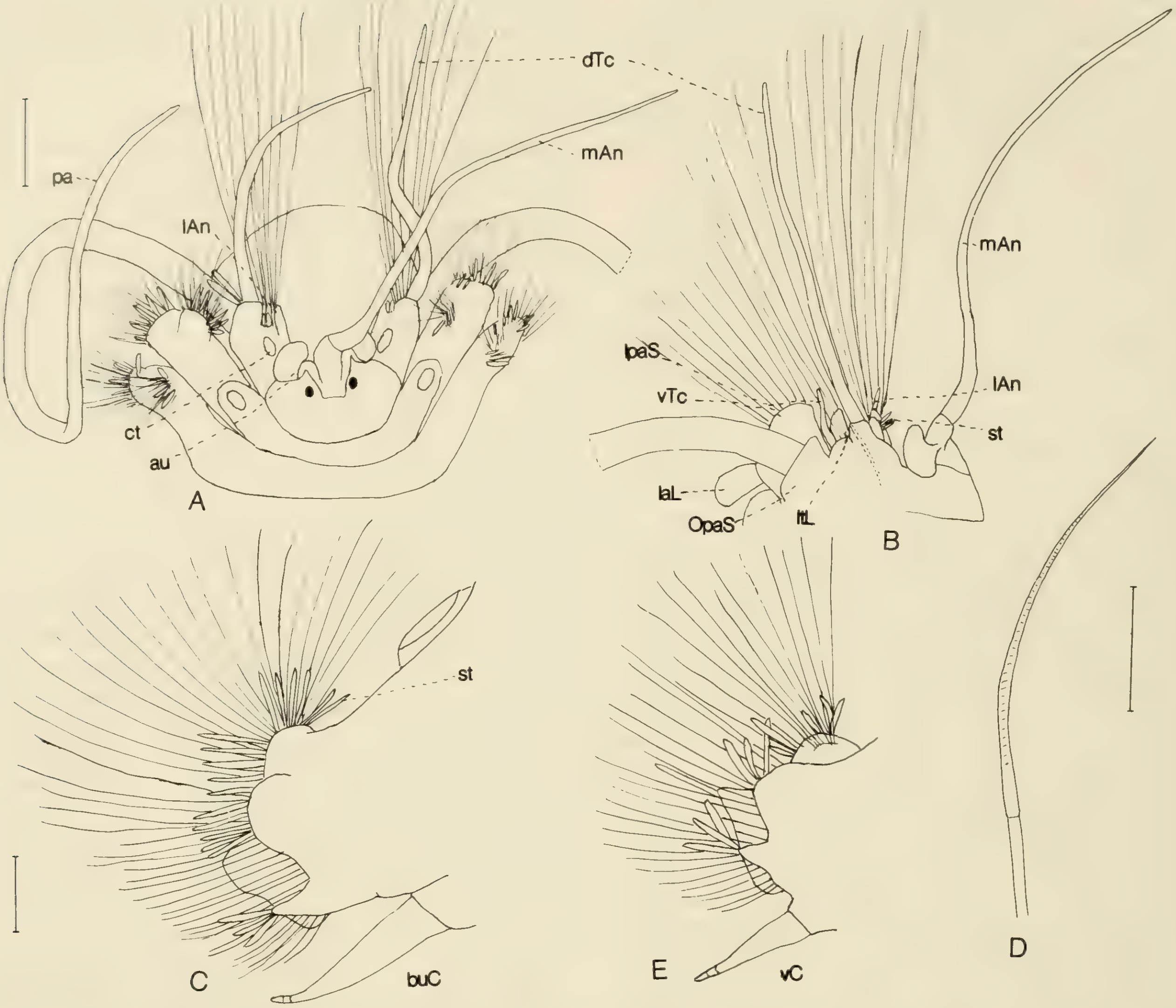

Fig. 3. *Labiosthenolepis sibogae,* syntype of *Leanira sibogae* (ZMA 526.2): A, Dorsal view of anterior end, pharynx partially extended, large anterior pair of eyes hidden by auricles on ceratophore of median antenna; B, Lateral view of prostomium, right I, and labial lobe on lateral lip, aciculum dotted, palp partially shown; C, Left elytrigerous parapodium from segment II, posterior view; D, Middle neuroseta from same; E, Left parapodium from segment III, posterior view. Scales = 0.5 mm for A, B; 0.2 mm for C, E; 0.1 mm for D. For abbreviations, see Fig. 1.

parapodia, with longer inner and shorter outer palpal sheaths; tentaculophores with long dorsal and short ventral tentacular cirri; setal lobe with single aciculum and well-developed bundle of capillary setae, directed anteriorly; without inner tentacular lobes. Buccal segment (II) with first pair of elytra and elytrophores, biramous parapodia with stylodes; buccal cirri thicker and longer than following ventral cirri; lateral lips of ventral mouth with fleshy or flat plate-like labial lobes. Segment III without dorsal cirri or dorsal tubercles. Parapodia biramous; notopodia with subdistal bract with circlet of stylodes; notosetae capillary, finely to coarsely spinose; neuropodia with subconical presetal acicular lobe and bilobed postsetal lobe with stylodes; neurosetae compound spinigers, with blades rather short, canaliculate, tapering to fine tips; with or without few additional simple spinose neurosetae. Ventral cirri short, tapered, with rounded basal knob. Pharynx with 11 pairs of border papillae and 2 pairs of jaws. Pygidium with pair of long anal cirri.

Remarks.—*Labioleanira* agrees with

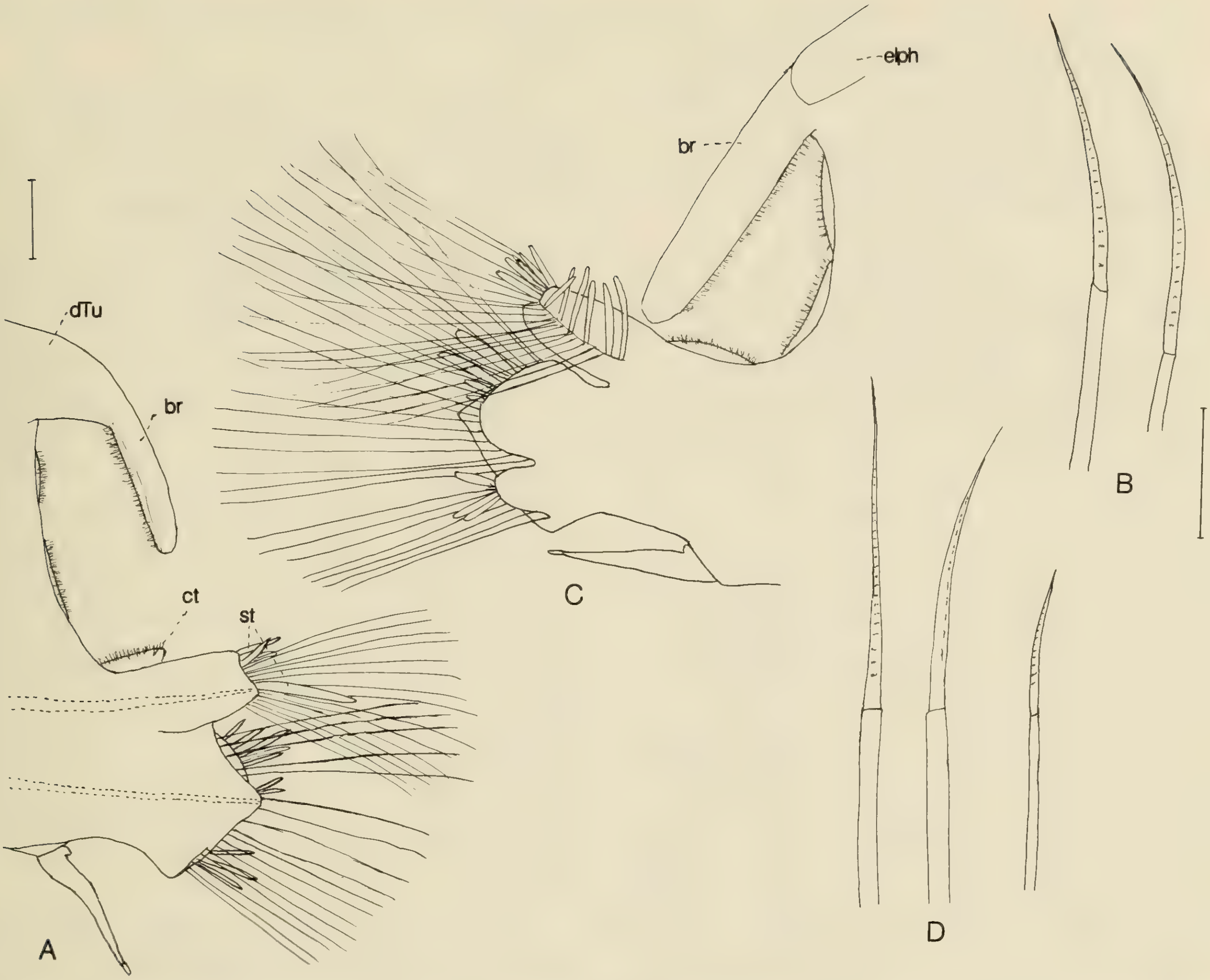

Fig. 4. *Labiosthenolepis sibogae,* syntype of *Leanira sibogae* (ZMA 526.2): A, Left anterior parapodium with dorsal tubercle, anterior view, acicula dotted; B, Middle and lower neurosetae from same; C, Left middle elytrigerous parapodium, posterior view; D, Middle and lower neurosetae from same. Scales = 0.2 mm for A, C; 0.1 mm for B, D. For abbreviations, see Fig. 1.

Leanira Kinberg, 1856 (limited) and *Ehlersileanira* Pettibone, 1970b in lacking inner tentacular lobes and dorsal ctenidia on segment I, and in lacking dorsal cirri and dorsal tubercles on segment III. *Labioleanira* differs from *Ehlersileanira* in having labial lobes on the lateral lips of the ventral mouth, instead of lacking labial lobes and in having the style of the median antenna long, instead of very short. *Labioleanira* differs from *Leanira* in having the ceratophore of the median antenna distinct and with lateral auricles, instead of lacking lateral auricles. Some species of *Leanira* agree with *Labioleanira* in having labial lobes on the lateral lips, such as *L. quatrefages* Kinberg, the type species of *Leanira, L. hystricis* Ehlers, and *L. adenensis* Pettibone.

Etymology.—*Labio,* labrum or lip, plus *Leanira,* in reference to the labial lobes on the lateral lips of the ventral mouth and its close relationship to *Leanira.*

Labioleanira yhleni (Malmgren, 1867), new combination
Figs. 5, 6

Leanira yhleni Malmgren, 1867:140.—Tebble, 1955:77.—Intes & Le Loeuff, 1975:289.

Leanira yhleni Malmgen?—McIntosh, 1876: 409, pl. 73: fig. 9.

Sthenolepis yhleni.—Hartman, 1965:14 (Catalogue).—Campoy, 1982:98, pl. 6: figs. H, I.—Kirkegaard, 1983:200, fig. 3A–D.

[Not *Leanira yhleni.*—Rullier, 1965: 171. =*Labiosthenolepis sibogae* (Horst)].

Remarks.—*Leanira yhleni* was incompletely described by Malmgren (1867) and the holotype (NRS) is in poor condition. Some specimens in the BMNH from a *Porcupine* station off N.W. Spain, identified by McIntosh (1876), serve to supplement the description. *L. yhleni* was referred to *Sthenolepis* by Hartman (1965:14), in her Catalogue; this was followed by Campoy (1982: 98), Kirkegaard (1983:200), and others. Some of the widely distributed records of the species need to be checked.

Material examined.—Northeast Atlantic Ocean: Ile de Ré near La Rochelle, France, 1865, G. von Yhlen, collector, holotype (NRS 599). Off Cape Finisterre, N. W. Spain, 146 m, *Porcupine* sta 10, 1870, 14 specimens (BMNH 1921:5:659–665; USNM 49564, ident. by McIntosh 1876). Off Accra, Ghana West Africa, 41.4 m, Buchanan Survey, 1 specimen (BMNH 1953.3.1.608, ident. by Tebble, 1955). France, *Andrée* sta III, 14 Aug 1922, Monod, collector, 4 specimens (MNHNP, collection of P. Fauvel & F. Rullier). Tyrrhenian Sea, 50–75 m, soft bottom, 1977, M. C. Gambi, collector, 2 specimens (collection M. C. Gambi).

Type material.—The holotype is an incomplete, flaccid specimen, 65 mm long, 5 mm wide, including setae, and 95 segments.

Description.—Complete specimen from *Porcupine* sta 45 mm long, 4 mm wide with setae, about 120 segments; incomplete specimen with 58 segments, 35 mm long, 5 mm wide. Body subquadrangular, flattened dorsoventrally, tapering gradually posteriorly. Elytra large, covering mid-dorsum except anteriorly; first pair small, rounded, becoming elongate oval to subcordiform; thin, transparent, without tubercles or papillae; with rounded opaque area posterolateral to place of attachment to elytrophore (Fig. 6E–H).

Prostomium and tentacular segment (I) fused basally; prostomium oval, wider than long; ceratophore of median antenna large, cylindrical, with pair of prominent lateral auricles and long tapering style; lateral antennae short, bilobed, fused to dorsal inner sides of I; posterior pair of eyes lateral to base of ceratophore; much larger anterior pair of eyes hidden from view dorsally by lateral auricles; palps very long, emerging ventral to I, with large rounded inner and shorter, rounded outer palpal sheaths; tentaculophores each with single aciculum, long, tapering dorsal tentacular cirrus, similar to but longer than median antenna, and short ventral tentacular cirrus; acicular lobe with 2 groups of long capillary setae extending anteriorly; without inner tentacular lobes; dorsal side of I without ctenidium, with 1–4 short stylodes between base of dorsal tentacular cirrus and lateral antenna (Fig. 5A–C).

Segment II or buccal segment with large, oval labial lobes on lateral lips of ventral mouth (Fig. 5B, C); biramous parapodium with notopodium rounded, with circlet of filiform stylodes and radiating bundle of long capillary notosetae; larger neuropodium with numerous stylodes and fan-shaped bundle of compound spinigerous neurosetae; ventral buccal cirri thick, tapered and longer than following ventral cirri (Fig. 5A, B, D). Segment III without dorsal cirri or dorsal tubercles (Fig. 5A); parapodia similar to II but with fewer stylodes and smaller ventral cirri (Fig. 5E); neurosetae compound spinigers with blades rather long, canaliculate, lower ones more slender than upper ones (Fig. 5F).

More posterior parapodia with branchiae attached to dorsal tubercles or elytrophores, beginning about segment 8–12, rudimentary more anteriorly; parapodial ctenidia dorsal to notopodium, 3 per parapodium, rather small, beginning about segment 8–16 (Fig. 6A, C). Notopodium cylindrical, with

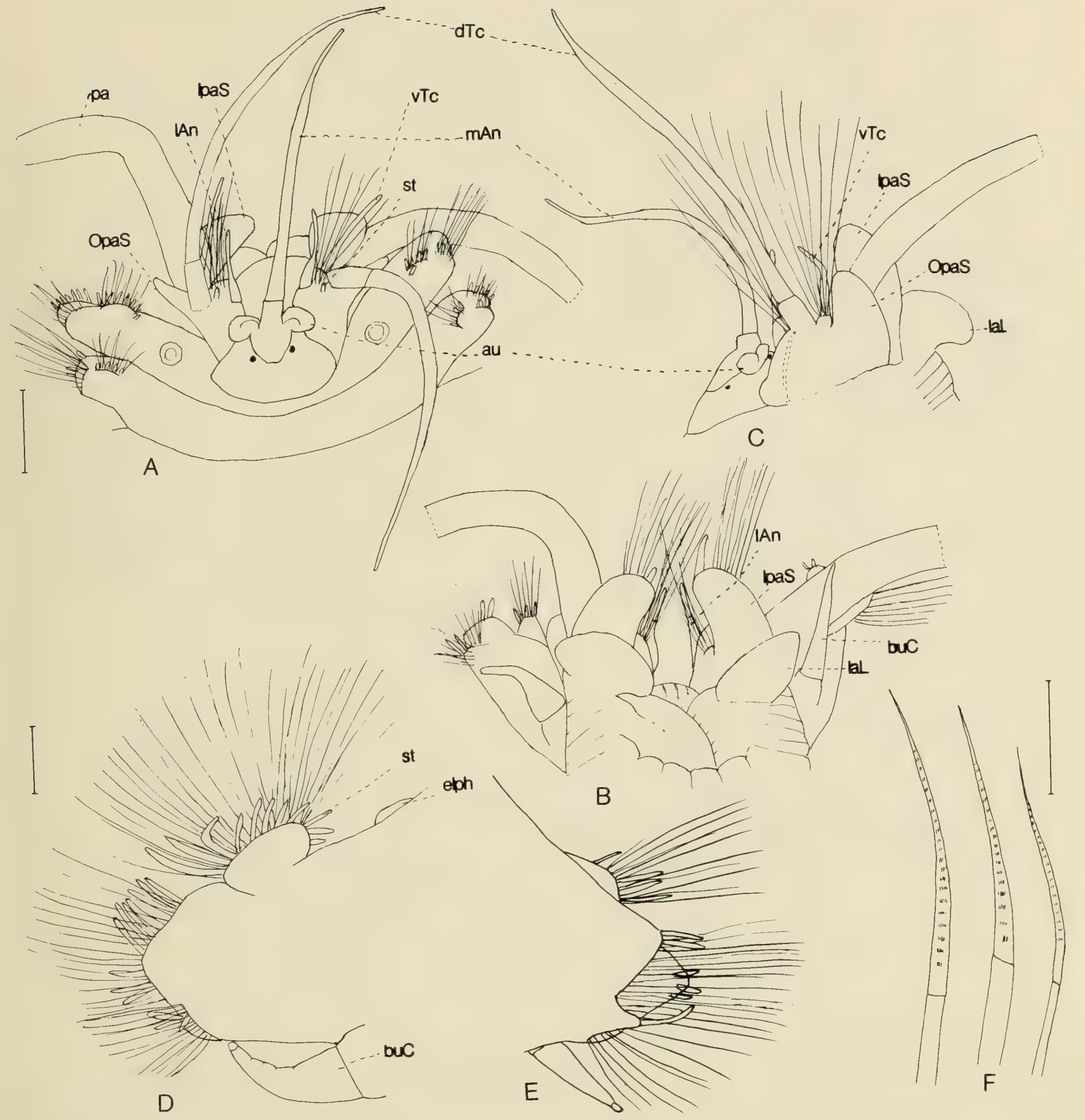

Fig. 5. *Labioleanira yhleni,* specimens from *Porcupine* sta. (USNM 49564, from BMNH 1921.5.659–665): A, Dorsal view of anterior end, pharynx partially extended, larger anterior pair of eyes hidden from view, tips of long palps not shown; B, Ventral view of anterior end of another specimen; C, Lateral view of prostomium, right I, and labial lobe on lateral lip; D, Right elytrigerous parapodium of segment II, anterior view; E, Right parapodium of segment III, posterior view; F, Upper, middle and lower neurosetae from same. Scales = 0.5 mm for A–C; 0.2 mm for D, E; 0.1 mm for F. For abbreviations, see Fig. 1.

circlet of stylodes on subdistal bract and large digitiform distal stylode; larger neuropodium with presetal conical acicular lobe and bilobed postsetal lobe with upper and lower groups of stylodes; ventral cirrus short, with basal knob and articulated tip (Fig. 6A, C). Neurosetae all compound spinigers with rather long canaliculate blades, lower ones more slender than upper ones (Fig. 6B, D).

Distribution.—North-east Atlantic Ocean, France, Spain Mediterannean Sea, West Africa, in 1–1900 m.

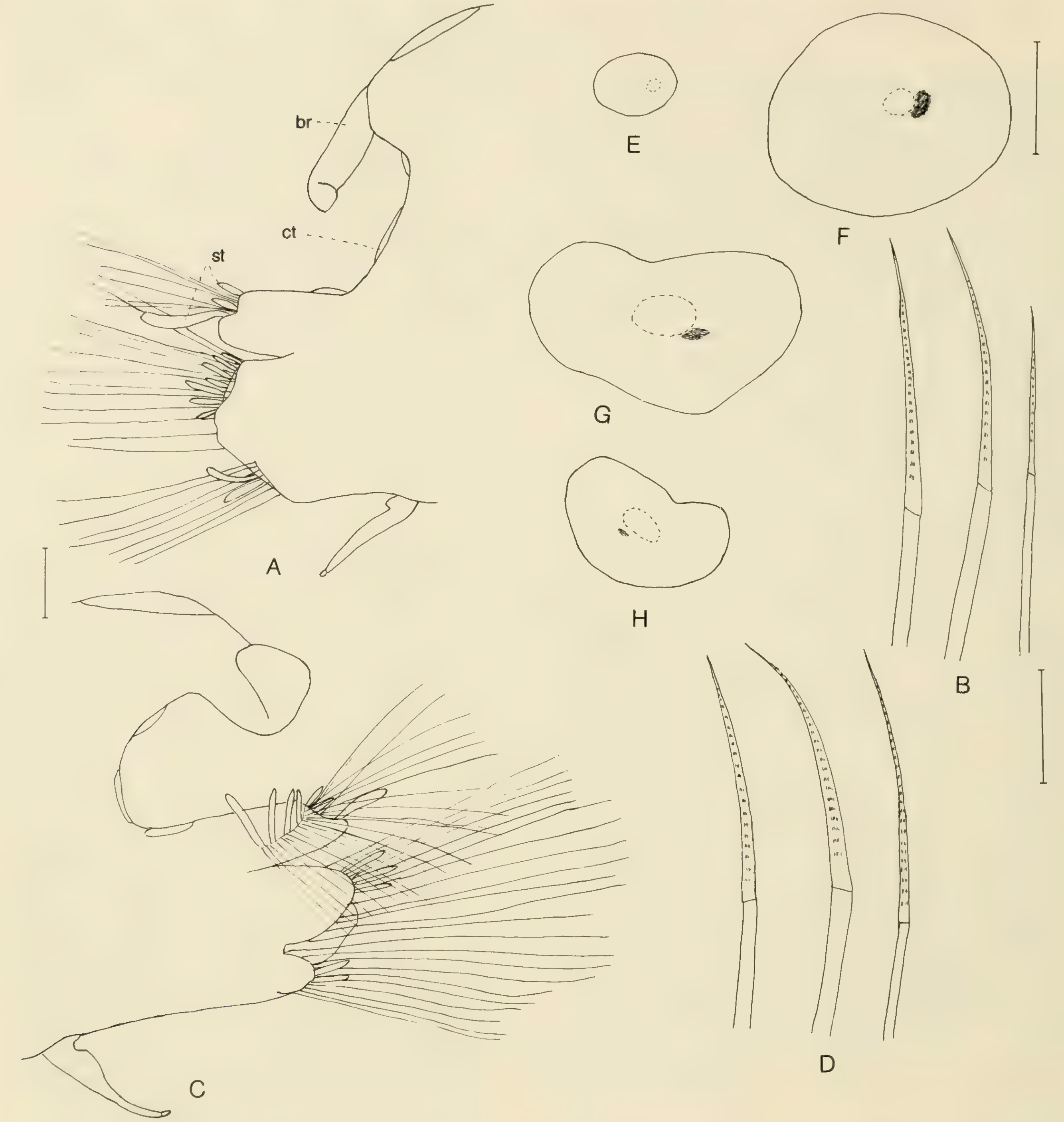

Fig. 6. *Labioleanira yhleni,* specimen from *Porcupine* sta (USNM 49564, from BMNH 1921.5.659–665): A, Right anterior parapodium, anterior view; B, Upper, middle and lower neurosetae from same; C, Right middle parapodium, posterior view; D, Upper, middle and lower neurosetae from same; E, Right 1st elytron; F, Right anterior elytron; G, Right middle elytron; H, Left posterior elytron. Scales = 0.2 mm for A, C; 0.1 mm for B, D; 1.0 mm for B–H. For abbreviations, see Fig. 1.

Labioleanira tentaculata (Horst, 1917), new combination
Figs. 7, 8

Leanira tentaculata Horst, 1917:117, pl. 24: figs. 4, 5. Hartman, 1959:116 (Catalogue).
Sthenelais luxuriosa.—Treadwell, 1920:592 (part; *Albatross* sta D5257). Not Grube, 1875.
Sthenolepis tentaculata.—Hartman, 1965: 14 (Catalogue).—Wu & Chen, 1985:72.

Material examined.—Malay Archipelago, *Siboga* stations: Java Sea, 06°16′5,

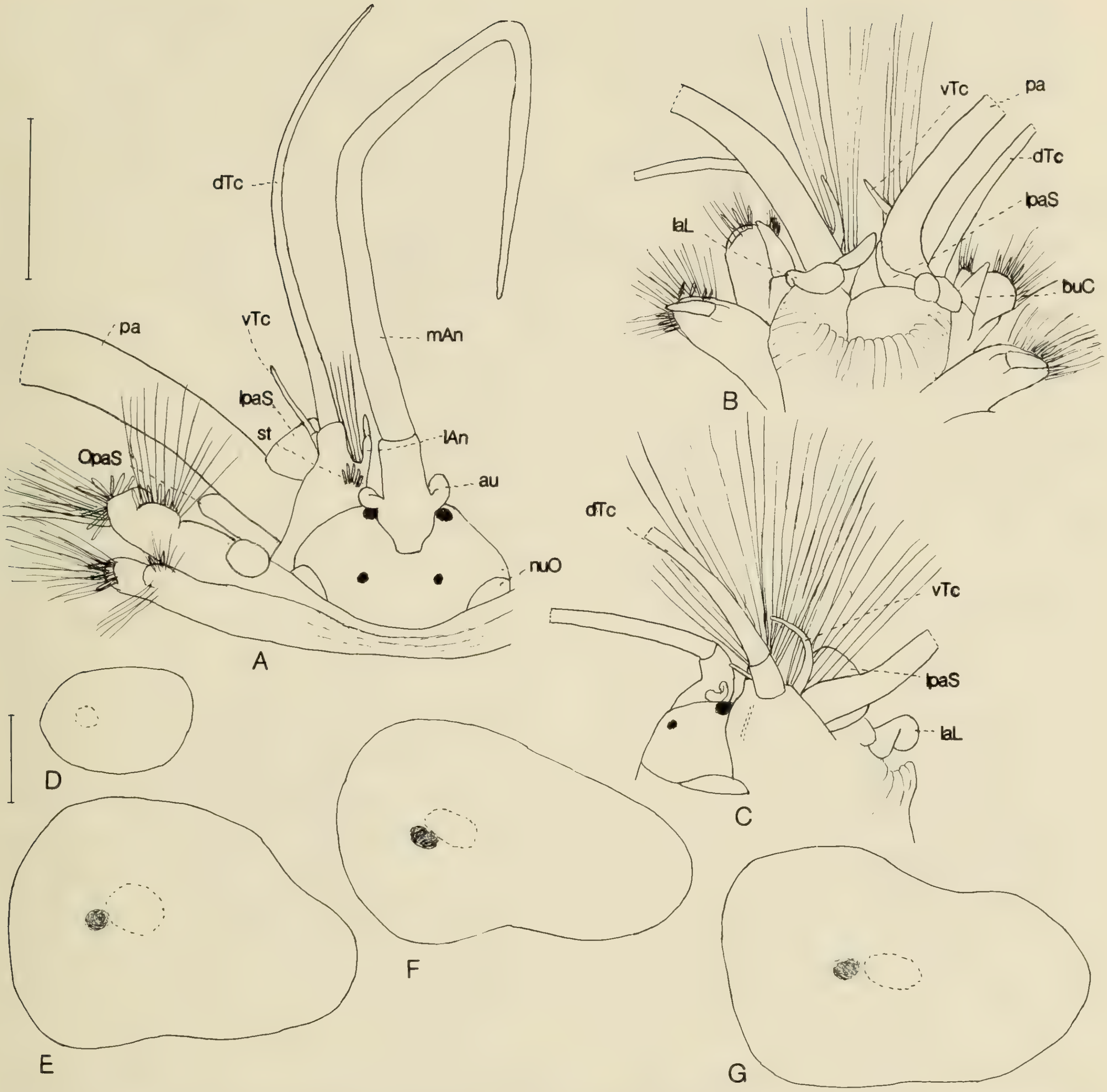

Fig. 7. *Labioleanira tentaculata* (syntypes of *Leanira tentaculata*: A, ZMA 528.1; B, C, ZMA 528.2; D–F, RMNH 1165): A, Dorsal view of anterior end (right side had been cut off), pharynx partially extended, tip of palp not shown; B, Ventral view of anterior end, tips of palps and dorsal tentacular cirri not shown; C, Lateral view of prostomium, tentacular lobe (I), and labial lobe on lateral lip (II), tips of palp, median antenna and dorsal tentacular cirrus not shown, aciculum dotted; D, Left 1st elytron; E, Left 6th elytron; F, Left middle elytron; G, Left posterior elytron. Scales = 1.0 mm for A–C; 0.5 mm for D–G. For abbreviations see Fig. 1.

114°37′E, 82 m, fine yellowish grey mud, sta 319, 22 Feb 1900, syntype of *L. tentaculata* (ZMA 528.1); 2 syntypes (RMNH 1165). 06°05′S, 114°07′E, 82 m, fine grey mud, sta 320, 23 Feb 1900, 2 syntypes of *L. tentaculata* (ZMA 528.2).

Philippine Islands, Southern Mindanao, eastern Illana Bay, 51 m, *Albatross* sta D5257, 22 May 1908, 3 specimens (USNM 17515, as *S. luxuriosa* by Treadwell, 1920).

Type material.—The five syntypes are incomplete, with more than 50 segments, 25 mm long and 5 mm wide, with setae.

Description.—Elytra large, nearly covering dorsum, small and oval on anterior few segments, becoming progressively larger and subpyriform in shape, thin, transparent, with opaque spots lateral to their place of attachment (Fig. 7D–G). Prostomium and tentacular segment (I) fused basally; prosto-

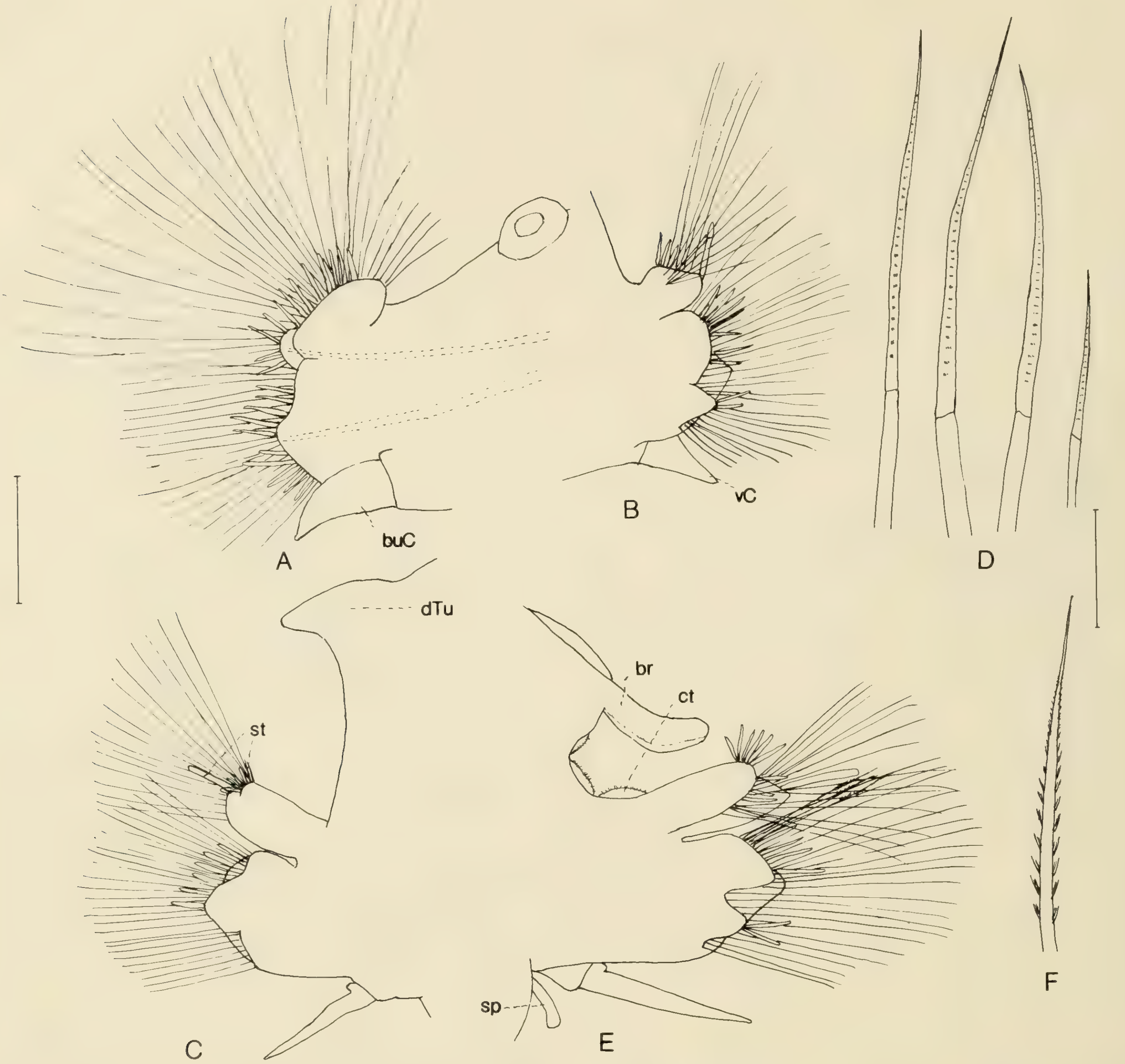

Fig. 8. *Labioleanira tentaculata* (syntype of *Leanira tentaculata,* ZMA 528.1): A, Right elytrigerous parapodium of segment II, anterior view, acicula dotted; B, Right parapodium of segment III, posterior view; C, Right parapodium from anterior region with dorsal tubercle, anterior view; D, Upper, middle and lower neurosetae from same; E, Right parapodium from middle region, posterior view; F, Simple neuroseta from same. Scales = 0.5 mm for A–C, E; 0.1 mm for D, F. For abbreviations, see Fig. 1.

mium oval, wider than long; ceratophore of median antenna large, cylindrical, with pair of small lateral auricles and long tapering style: lateral antennae short, bilobed, fused to dorsal inner sides of I: posterior pair of eyes in middle of prostomium; larger anterior pair of eyes below small antennal auricles and not hidden from view; palps very long, emerging ventral to I, with large, oval inner and low, outer palpal sheaths; tentaculophores each with single aciculum, long tapering dorsal tentacular cirrus, similar to but shorter than median antenna, and much shorter ventral tentacular cirrus; acicular lobe with 2 groups of long capillary setae extending anteriorly; without inner tentacular lobes; dorsal side of segment I with about 6 short stylodes between base of dorsal tentacular cirrus and lateral antenna (Fig. 7A, C; Horst 1917, pl. 24: fig. 4).

Segment II with semicircular nuchal organs and thick, fleshy labial lobes on lateral lips of ventral mouth (Fig. 7A–C); biramous parapodium with notopodium rounded, with circlet of filiform stylodes and radiating bundle of long capillary notosetae; larger neuropodium with numerous stylodes and fan-shaped bundle of compound spinigerous neurosetae; ventral buccal cirri thick, tapered, and longer than following ventral cirri (Figs. 7A, B, 8A). Segment III without dorsal cirri or dorsal tubercles (Fig. 7A; Horst, 1917, pl. 24: fig. 4); parapodia similar to II but with fewer stylodes and smaller ventral cirri (Fig. 8B).

More posterior parapodia with branchiae attached to dorsal tubercles or elytrophores, beginning about segment 19–25, rudimentary more anteriorly; parapodial ctenidia, dorsal to notopodium, 3 per parapodium, low, nearly contiguous, beginning about segment 19 (Fig. 8E). Notopodium cylindrical, with circlet of stylodes on subdistal bract and large digitiform distal stylode; larger neuropodium with presetal conical acicular lobe and bilobed postsetal lobe, with upper and lower groups of stylodes; short ventral cirrus with basal knob (Fig. 8C, E; Horst 1917, pl. 25: fig. 5). Neurosetae compound spinigerous, with long canaliculate blades, lower ones shorter and more slender (Fig. 8D); some middle parapodia with few upper simple neurosetae with spirally arranged spinose whorls (Fig. 8E, F). Tubular segmental papilla, near base of ventral cirrus, beginning about segment 30 (Fig. 8E).

Distribution.—West-Central Pacific Ocean, Indonesia, Philippines, South China Sea, in 51–82 m.

Key to the Two Genera and Four Species of Sigalionidae Covered Herein

1. Segment I with L-shaped inner tentacular lobes medial to tentaculophores (Figs. 1C, D, 3B). Dorsal sides of segment I with oval ctenidia (Figs. 1A, 3A). Segment III with (Fig. 1A, G) or without (Fig. 3A) small dorsal tubercles .... *Labiosthenolepis,* new genus 2

– Segment I without inner tentacular lobes medial to tentaculophores (Figs. 5C, 7C). Dorsal sides of segment I without ctenidia (Figs. 5A, 7A). Segment III without dorsal tubercles (Figs. 5A, 7A) .... *Labioleanira,* new genus 3

2. Labial lobes on lateral lips of segment II thick, fleshy, lobulate (Fig. 1B–D). Dorsal sides of segment I without stylodes (Fig. 1A). Segment III with small dorsal tubercles and distal papilla (Fig. 1A, G). Blades of compound spinigerous neurosetae in middle parapodia short (Fig. 2D) ... *Labiosthenolepis laevis* (McIntosh), new combination

– Labial lobes on lateral lips of segment II oval, thin, flattened (Fig. 3B). Dorsal sides of segment I with few, short stylodes between bases of dorsal tentacular cirri and lateral antennae (Fig. 3A). Segment III without dorsal tubercles (Fig. 3A). Blades of compound spinigerous neurosetae of middle parapodia long (Fig. 4D) .. *Labiosthenolepis sibogae* (Horst), new combination

3. Prostomium with lateral auricles on ceratophore of median antenna large, hiding anterior pair of large eyes; posterior pair of small eyes lateral to base of ceratophore (Fig. 5A). Dorsal sides of segment I with single small stylode between bases of tentacular cirri and lateral antennae (Fig. 5A). Without nuchal organs (Fig. 5A). Labial lobes on lateral lips of segment II oval, flattened (Fig. 5B, C). Middle parapodia without additional single neurosetae .... *Labioleanira yhleni* (Malmgren), new combination

– Prostomium with lateral auricles on ceratophore of median antenna small, not hiding anterior pair of large eyes; posterior pair of small eyes in middle of prostomium (Fig. 7A). Dorsal sides of segment I with

5 or so stylodes between bases of dorsal tentacular cirri and lateral antennae (Fig. 7A). With semicircular nuchal organs (Fig. 7A, B). Labial lobes on lateral lips of segment II, thick, fleshy, lobulated (Fig. 7B, C). Middle parapodia with additional simple spinose neurosetae (Fig. 8F) ..... *Labioleanira tentaculata* (Horst), new combination

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PSEUDOPOLYDORA DIOPATRA, A NEW SPECIES (POLYCHAETA: SPIONIDAE) FROM TAIWAN

Hwey-Lian Hsieh

Abstract.—A new spionid polychaete species is described from a sandflat on the west coast of Taiwan. *Pseudopolydora diopatra* lives on the tube-caps of the onuphid *Diopatra bilobata.* The species is very similar to *Pseudopolydora paucibranchiata.* Both species are small in size (3–6 mm), have similar setal types on the fifth setiger, and a cup-shaped pygidium. The new species differs from the latter in lacking median antenna, in having fewer pairs of branchiae (5–6 pairs vs. 9–11 pairs), and fewer major setae (4–5 hooks and 6–8 pennoned setae vs. 8–9 hooks and 10 pennoned setae) on setiger 5.

A detailed study of the polychaete fauna from the intertidal areas on the west coast of Taiwan has recently been conducted. The onuphid *Diopatra bilobata* Imajima is one of the most obvious tube-dwellers on the sandflats (Hsieh & Chang 1991). A new *Pseudopolydora* species has been found in association with the tube-caps of *D. bilobata* (Hsieh & Chang 1991). This species is herein described and compared with related species of the genus. The types are deposited in the Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZIP), and the National Museum of Natural History, Smithsonian Institution (USNM).

Family Spionidae

Genus *Pseudopolydora* Czerniavsky

Pseudopolydora diopatra, new species

Figs. 1–10

Material examined.—Intertidal sandflat at Hsiang Shan (24°50′N, 120°54′E), Hsin Chu Hsien, northwest coast of Taiwan, Nov 1990, holotype (ASIZIP 9011HS1); 23 paratypes, May 1990 (ASIZIP 9005HS); 14 paratypes, Nov 1990 (ASIZIP 9011HS); 42 paratypes, Nov 1990 (USNM 142034); 10 paratypes, May 1991 (ASIZIP 9105HS-SEM).—Intertidal sandflat at Tung Hsio (24°30′N, 120°37′E), Miao Li Hsien, west coast of Taiwan, 20 paratypes, Jun 1988 (ASIZIP 8806TH); 15 paratypes, Sep 1991 (ASIZIP 9109TH).

Description.—Specimens small; holotype (male) measuring 2.8 mm long, 0.3 mm wide at setiger 5, for 23 setigers (Fig. 1). Paratypes including 25 males, 30 females, 2 juveniles measuring 2.4–2.9 mm long, 0.3–0.5 mm wide at setiger 5, for 20–34 setigers. Dorsal transverse ciliary bands present on setigers 7–10 (see Fig. 10). Black pigmented, ventral transverse bands present on setigers 3–10 of formalin preserved specimens.

Prostomium bifurcate anteriorly (Fig. 2). Caruncle keel–like, extending to posterior edge of setiger 2 (Fig. 2); pair of brown pigment spots sometimes present on posterior caruncle. Eyes numbering 2 pairs, located anterior to palpal bases. Occipital antenna absent. Nuchal organs present posteriorly to palps, lateral to caruncle (Fig. 2). Palps in live specimens with 10–12 transverse yellow bands. Ventral grooves of palps ciliated (Fig. 3). Ventral prostomial surface bearing 1 patch of cilia (Fig. 3).

Notopodia of setiger 1 reduced to small digitiform lobes arising from palpal bases, without setae; neuropodia also reduced, larger than notopodial lobes, with capillary setae (Fig. 2). Subsequent noto- and neuropodia well developed. All notosetae as limbate capillaries, most numerous on setigers 2-9 (Fig. 4). Neurosetae of setigers 2–7 as limbate capillaries with fine spines (Fig. 5); broader, shorter, more curved than notosetae in same setigers. Bidentate hooded hooks with constricted shafts, first present from setiger 8, numbering 10–11 per fascicle; apical tooth closely apposed to main fang (Fig. 6). Presetal noto- and neuropodial lamellae of anterior setigers poorly developed; postsetal lamellae forming small lobes (Fig. 7). Major setae of setiger 5 arranged in 2 C-shaped rows: dorsal most row with 4–5 stout falcate hooks (Figs. 7, 8, 9b); ventral most row with 6–8 pennoned setae lacking bristles or flanges (Figs. 7, 8, 9a).

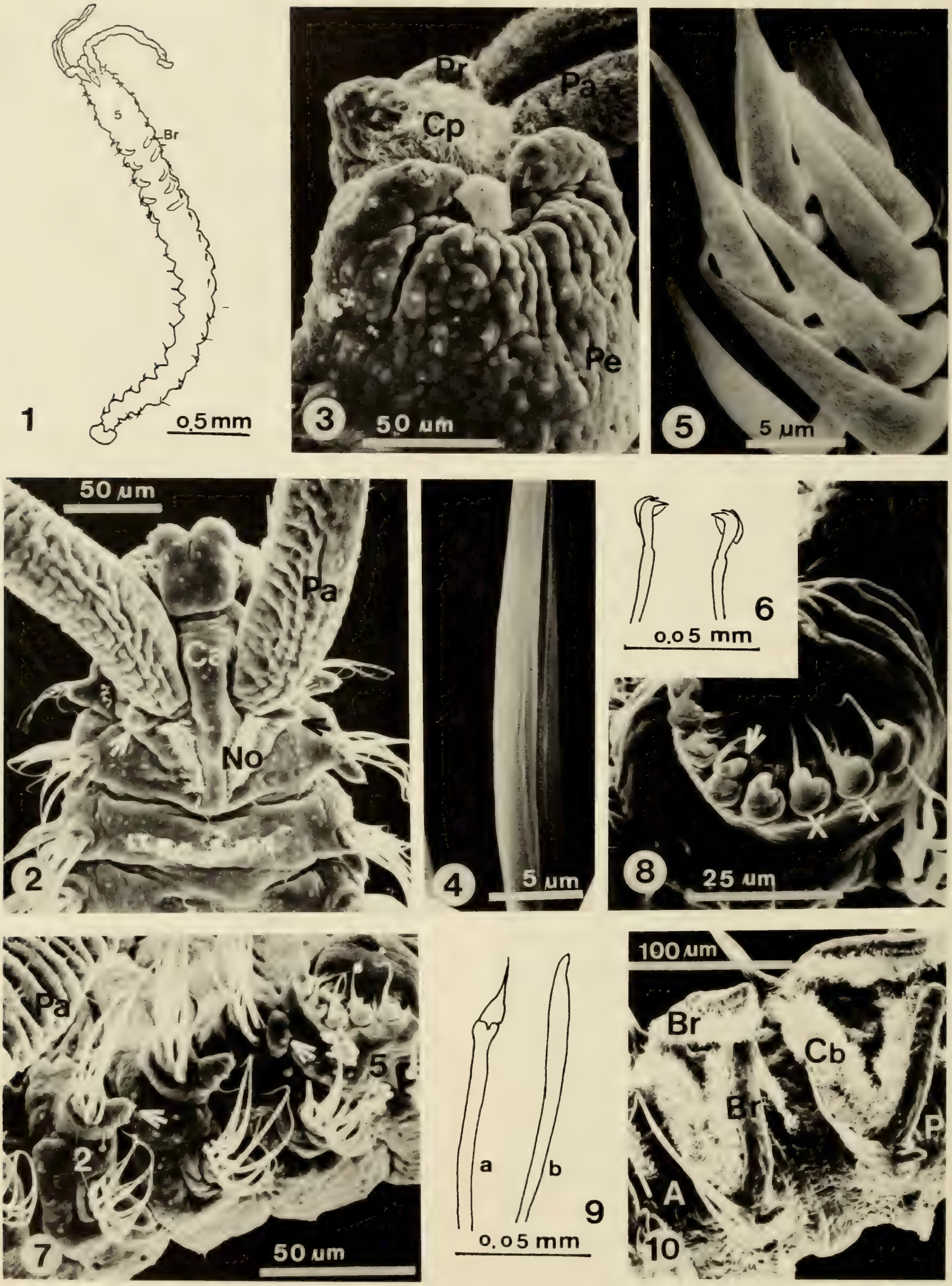
Branchiae numbering 5–6 pairs, present on setigers 7–11 or 12, sometimes unequally distributed on right and left sides of body; inner lateral margins heavily ciliated (Fig. 10).

Remarks.—Twelve species of *Pseudopolydora* have been previously recorded, including *P. antennata* (Claparede) (Okuda 1937), *P. corallicola* Woodwick, 1964, *P. gibbsi* Light, 1974, *P. glandulosa* Blake & Kudenov, 1978, *P. kempi* (Southern) (Berkeley & Berkeley 1954; Imajima & Hartman 1964; Light 1969, 1978; Banse 1972), *P. paucibranchiata* (Okuda) (Okuda 1937, Imajima & Hartman 1964), *P. pigmentata* Woodwick, 1964, *P. primigenia* Blake, 1983, *P. prolifera* (Augener) (Blake & Kudenov 1978), *P. pulchra* (Carazzi) (Eleftheriou 1970), *P. smurovi* Tzetlin & Britayev, 1985, and *P. stolonifera* Blake & Kudenov, 1978. Another four species, *P. bassarginensis* (Zachs) (see Uschakov 1955), *P. derjugini* (Zachs) (see Hartman 1959, 1965), *P. novaegeorgiae* Gibbs (see Blake & Kudenov 1978), and *P. orientalis* (Annenkova) (see Uschakov 1955) are incompletely known. *Pseudopolydora reishi* (Woodwick) has been transferred to the genus *Carazziella* (Blake 1979). Thus, these five species are not included for further discussions.

Pseudopolydora diopatra resembles *Pseudopolydora paucibranchiata* (Okuda 1937, Imajima & Hartman 1964) in that the tear-drop-shaped pennoned setae and stout hooks of setiger 5 are sharply tapered and slightly curved, respectively. Both species are moderately small (*P. diopatra* 2–3 mm long; *P. paucibranchiata* 4–6 mm long), and have funnel-shaped pygidia with a dorsal notch. *P. diopatra* differs from *P. paucibranchiata* in having a bifurcate, instead of a rounded, entire prostomium; lacking an occipital antenna; and in having fewer branchiae (5–6 instead of 9–11 pairs). *P. diopatra* also differs from all other members of the genus in such features as setal morphology, numbers of branchiae, prostomial morphology, caruncle length, and shape of the pygidium. The following key to the known species of *Pseudopolydora* reflects these differences. Characters used in this key are modified from those in Blake & Kudenov's study (1978):

Key to Known Species of *Pseudopolydora*

1. Maximal number of segments 15–16; small, up to 3 mm long 2
– Maximal number of segments greater than 20; small to large, up to 30 mm long 4
2. Ends of pennoned setae from setiger 5 bristled; ends not distally enlarged, curved or broom-like ... 3
– Ends of pennoned setae from setiger 5 not bristled; ends distally enlarged, curved, broom-like ... . *P. smurovi*
3. Pennoned setae of setiger 5 with long apex and fenestrated edge surrounding a cavity; prostomium entire .... *P. prolifera*
– Pennoned setae of setiger 5 with expanded apex; lacking fenestrated edge surrounding a cavity; prostomium incised .... *P. stolonifera*
4. Prostomium entire 5
– Prostomium incised 7



Figs. 1–10. 1. *Pseudopolydora diopatra,* holotype (male). Dorsal view. Br: branchiae, numeral 5 indicating setiger 5; 2. *Pseudopolydora diopatra,* paratype, anterior end. Ca: caruncle, No: nuchal organ, Pa: palp, Arrows: projection of reduced first notopodium; 3. *Pseudopolydora diopatra,* paratype, ventral view of anterior end. Cp: ciliary patch, Pa: palp, Pe: peristomium, Pr: prostomium; 4. *Pseudopolydora diopatra,* paratype, limbate notosetal capillaries, setiger 8; 5. *Pseudopolydora diopatra,* paratype, limbate neurosetal capillaries, setiger 4; 6. *Pseudo-*

5. Occipital antenna present .... *P. paucibranchiata*
– Occipital antenna absent 6
6. Notosetae present on setiger 1; stout, sickle-shaped hooks present in posterior notopodia; strong falcate notosetae absent on setigers 4–5 .... *P. gibbsi*
– Notosetae absent on setiger 1; stout, sickle-shaped hooks absent in posterior notopodia; strong falcate notosetae present on setiger 4–5 .... *P. pigmentata*
7. Prostomium deeply incised, produced into conspicuously diverging lobes 8
– Prostomium weakly incised, not produced into conspicuously diverging lobes 11
8. Posterior notopodia with conical bundles of awl-shaped setae; setigers 6–7 each with paired internal glands .... *P. corallicola*
– Posterior notopodia without conical bundles of awl-shaped setae; setigers 6–7 each lacking paired internal glands 9
9. Pennoned setae of setiger 5 with apices short, tapered, and large subdistal concavities; pygidium notched dorsally and ventrally .. .. *P. antennata*
– Pennoned setae of setiger 5 with apices long, slender, curved, and narrow concavities; pygidium notched dorsally, not ventrally .. 10
10. Prostomium pigmented; caruncle indistinct, extending to setiger 2; pigment pattern absent on anterior setigers .... *P. pulchra*
– Prostomium not pigmented, caruncle distinct, extending to setiger 4; pigment pattern sometimes present on anterior setigers *P. kempi*
11. Branchiae with glands; hoods of hooded hooks striated *P. glandulosa*
– Branchiae without glands; hoods of hooded hooks not striated ... 12
12. Branchiae present on setiger 11 to 13–15, fused basally with notopodial lamellae; males with an additional pair of branchiae on setiger 2 .... *P. primigenia*
– Branchiae present on setigers 7 to 12–13, not fused basally with notopodial lamellae; males lacking an additional pair of branchiae on setiger 2 .... *P. diopatra*

Pseudopolydora diopatra is dioecious and constructs muddy tubes. Larvae are brooded by females in their tubes until they attain the three-setiger stage. After release, the larvae become planktotrophic. Competent larvae have 12–15 setigers and show preference for the tube-caps of the onuphid *Diopatra bilobata.* They are rarely found in sand surrounding the tubes of *Diopatra bilobata* (Hsieh & Chang 1991).

Etymology.—The specific name, *diopatra,* is based on the characteristics of the worms' habitat. *Pseudopolydora diopatra* was found to construct muddy tubes in the crevices of highly decorated tube-caps of *Diopatra bilobata* (Hsieh & Chang 1991).

Habitat.—The type locality is an intertidal sandflat on the northwest coast of Taiwan. Tubes of *Diopatra bilobata* protrude above the sediment. The habitat-habitant relationship between *D. bilobata* and *Pseu-*

←

polydora diopatra, paratype, bidentate hooded hooks, setiger 8; 7. *Pseudopolydora diopatra,* paratype, lateral view of setigers 1–5. Pa: palp, Numerals 2, 5: setiger 2, 5. Arrows: postsetal notopodial lamella; 8. *Pseudopolydora diopatra,* paratype, left setiger 5. Arrow: stout hook, X: pennoned seta; 9. *Pseudopolydora diopatra,* paratype, major setae on setiger 5. a, pennoned seta; b, hook; 10. *Pseudopolydora diopatra,* paratype, the dorsum of setigers 10–11. A: anterior, P: posterior, Br: branchia; Cb: ciliary band.

dopolydora diopatra is closely tied into granulometry of the sandflat and worms' tubes (Hsieh & Chang 1991). The median grain sizes of the flat range from 0.17 to 0.18 mm in diameter with modal sizes from 0.15 to 0.21 mm. Silt-clay content is little, less than 2% of dry weight. In contrast, the median particle sizes of *Diopatra* tube-caps are from 0.21 to 0.25 mm in diameter with modal particles larger than 1.00 mm. Silt-clay content in tube-caps is higher, usually up to 18–19% of dry weight. As regards the muddy tubes of *P. diopatra,* the median grain sizes range from 4.6 to 27.9 μm with modal sizes from 4.6 to 15.7 μm. These particles fall well in the category of silt and clay. The tube-caps harbor more silt and clay, in turn, providing *P. diopatra* material for tube construction and for feeding upon (Hsieh & Chang 1991).

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LURUS MINOS, THE FIRST SPECIES OF LURIDAE (TURBELLARIA: RHABDOCOELA) FROM THE OLD WORLD

Wolfgang Sterrer

Abstract.—*Lurus minos,* a new species of the recently erected statocyst-bearing family Luridae, was found in subtidal fine sand off the island of Crete (eastern Mediterranean). Of the four previously known species in the genus, three occur in the western Atlantic (Brazil and North Carolina) and one in Fiji. The new species differs in the sclerotized structures of the reproductive system, and seems most closely related to *L. tyndareus* from Fiji.

Described by Marcus (1950) as a new species and genus from the coast of Brazil, the microturbellarian *Lurus evelinae* has characteristics typical of Dalyellioida-Provorticidae but in addition possesses a statocyst, a structure not otherwise present in the Dalyellioida nor any other members of the order Rhabdocoela. On the basis of the discovery of three further species of *Lurus* (*L. castor, L. pollux* and *L. tyndareus*), Sterrer & Rieger (1990) erected the family Luridae to reflect this unusual combination of characters. Reinhard Rieger (pers. comm.) provided preliminary data on statocyst ultrastructure in *Lurus*; these suggest that, in spite of superficial similarities with Catenulida-Retronectidae (Sterrer & Rieger 1974) such as statolith size, shape, number and variability, the lurid statocyst is a large intracellular vacuole within a modified gut cell, and thus not homologous with the statocyst of any other turbellarian (cf. Ehlers 1985). The genus *Lurus,* therefore, continues to be of special interest for the study of platyhelminth phylogeny.

During a brief collecting trip to Crete in the summer of 1991, I found specimens belonging to a fifth species in this genus, the first to be reported from the shores of the Old World. Samples were collected by snorkeling over the shallow bottom and scooping sand into a bucket. Specimen extraction, documentation and analysis follow Sterrer (1971). This description is based on observation of live animals only. Wholemounts of squeezed specimens were preserved with formalin-glycerol and sealed with Eukitt.

Lurus minos, new species
Fig. 1A–H

Etymology.—After King Minos, the legendary ruler of bronze-age Crete.

Holotype.—Wholemount of one adult specimen in squeeze preparation, deposited with the Swedish Museum of Natural History in Stockholm (SMNH Type Coll. 4379).

Paratypes.—Wholemounts of 2 adult specimens in squeeze preparation, deposited with the US National Museum of Natural History (USNM 149923, 149924).

Type locality.—Crete (Eastern Mediterranean), Messaras Bay, beach W of Phaistós; very fine sand with ripple marks in 2–4 m depth, 10–100 m from shore; coll. 14 Sep 1991, 7 specimens.

Other localities.—Crete, south shore, beach E of Lerápetra; fine, clean sand with ripple marks in 0.5–3 m depth, 5–100 m from shore; coll. 15 Sep 1991, 1 specimen. North shore, inner harbor of Pánormos; fine sand with detritus in 1.5 m depth; coll. 18 Sep 1991, 1 specimen.

Diagnosis.—*Lurus* with single testis and

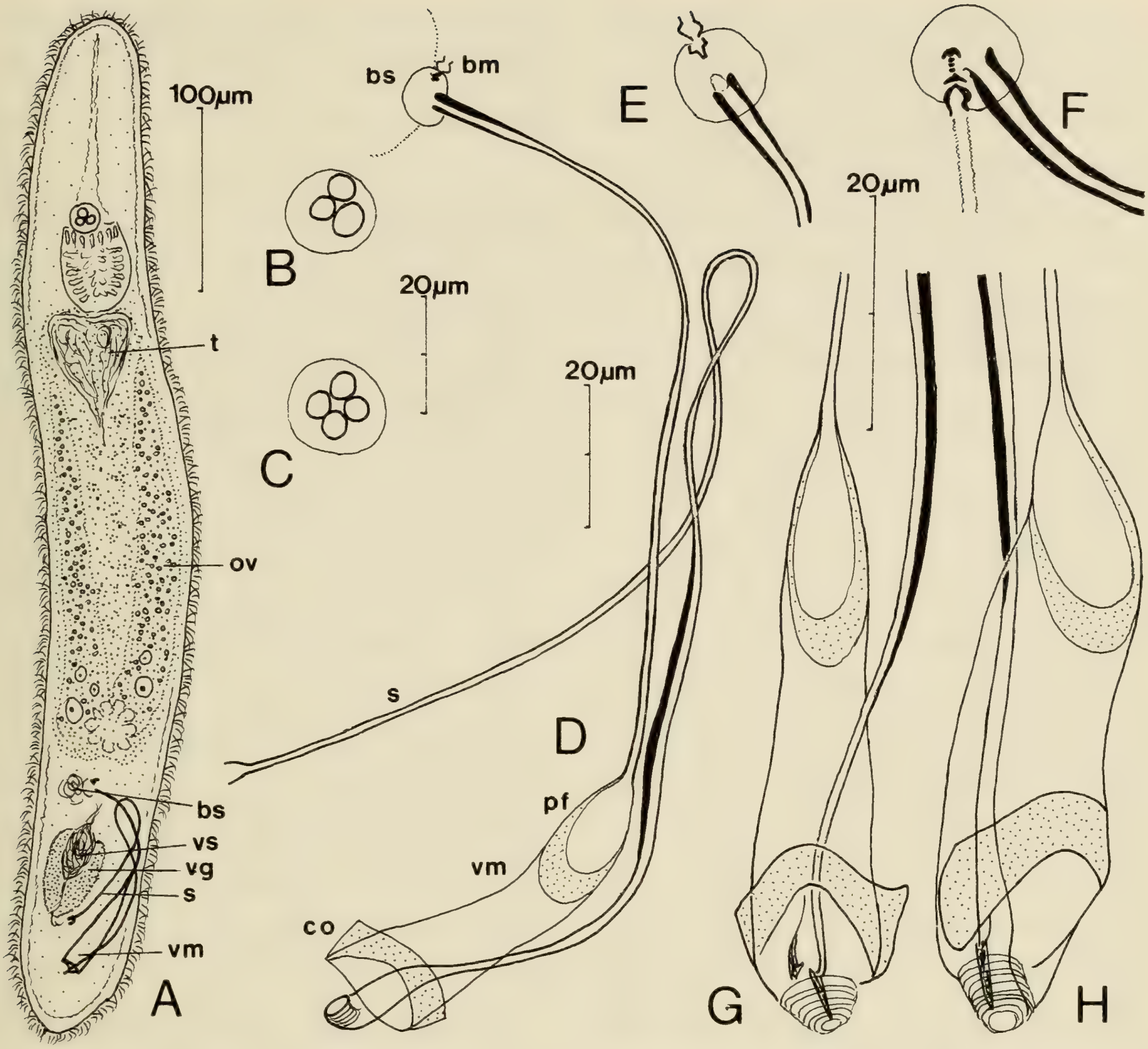

Fig. 1. *Lurus minos.* A, Habitus of adult; B and C, Statocyst of two specimens; D, Sclerotized parts of reproductive system; E and F, Proximal end of vagina mouthpiece with bursa mouthpiece of two specimens; G and H, Distal end of vagina mouthpiece and male copulatory stylet of two specimens. The scales apply to A, B–C, D, and E–H, respectively. Abbreviations: bm bursa mouthpiece, bs bursa, co collar of vagina mouthpiece, ov ovary, pf perforation of vagina mouthpiece, s male copulatory stylet, t testis, vg vesicula granulorum, vm vagina mouthpiece, vs seminal vesicle.

vas deferens. Copulatory stylet is a once-folded, 2 μm wide tube with a total length of 240 μm. Vagina mouthpiece is a slightly curved, 1–2 μm wide tube of 180 μm length, distally flared into a 50 μm long funnel with a collar. Bursa mouthpiece 5 μm long, delicate, attached to proximal end of vagina mouthpiece.

Description.—Organization and behavior: Colorless; the rostral third of body usually translucent, the rest opaque. Rather fusiform when swimming (Fig. 1A), more barrel-shaped when resting. Mature specimens are 275–500 μm long and 75–80 μm wide; the only juvenile measured 400 μm by 80 μm. As the animal swims it moves its head from side to side in a steady pendulum motion that seems characteristic for the genus.

Nervous and sensory system: A statocyst (Fig. 1B, C) was present in all specimens. It is located above the anterior part of the pharynx, spherical, 15 μm in diameter, and contains 3 or 4 more or less spherical statoliths of 5–7 μm diameter. Of the 9 specimens encountered, 7 contained 3 statoliths, and 2 contained 4, which gives a mean statolith number of 3.22 for the sample.

Reproductive system—male organs: There is a single, conical testis (Fig. 1A; t) located immediately behind and below the pharynx; a vas deferens was not seen but the shape of the testis suggests it is single as well. The bulbous seminal vesicle (vs) is surrounded by a finely granular vesicula granulorum (vg); it empties caudally into a male stylet (s). Proximally somewhat distended to form a narrow funnel, the male stylet (Fig. 1D; s) is a long, apparently flexible tube of about 2 μm diameter that first extends rostrally for about 100 μm, then makes a 180° turn to extend caudally for about 130 μm to join the vagina mouthpiece (vm) at the common genital opening (Fig. 1G, H). In a 50 μm long portion of this distal half the male stylet wall is thickened on one side. The total length of the male stylet is about 240 μm.

Female organs (Fig. 1A): The female gonads (ov) are paired, being vitellaria in the larger anterior part, and germaria (with large oocyte nuclei) in the posterior. The vagina mouthpiece (vm) is a 180 μm long tube, 1–2 μm wide, that runs from the bursa (bs) to the genital opening. Distally the vagina mouthpiece forms a 50 μm long and 18 μm wide funnel whose opening is bordered by a 5 μm wide collar (co). The narrow part of the funnel looked as if it had a large, oblong lateral perforation (pf). The male stylet makes contact with the funnel just below the collar, which it apparently traverses, and emerges beyond the rim of the vagina mouthpiece as a prominent papilla made up of concentric rings (Fig. 1G, H). Proximally, the vagina mouthpiece flares into a shallow saucer, to the rim of which a third sclerotized structure is attached, the bursa mouthpiece (Fig. 1D; bm). Difficult to resolve, the bursa mouthpiece looks somewhat like a roll of coins topped by a cup, all of which are presumably pierced by a central canal through which sperm pass to the oocyte (Fig. 1E, F).

Discussion.—Within the genus *Lurus,* to which it clearly belongs, *L. minos* is most closely associated with the three recently described species (*L. castor, L. pollux* and *L. tyndareus*) by the possession of only one testis, and the close proximity of vesicula seminalis and vesicula granulorum (in contrast to *L. evelinae* for which paired testes as well as separate vesiculae have been described). The sclerotized parts of the reproductive system are most similar to those of *L. tyndareus* and *L. castor.* In both species the joint terminal opening of male stylet and vagina mouthpiece are urn- or funnel-shaped, with a distinct collar and with concentric rings in *L. castor,* and with the male stylet terminating in a papilla in *L. tyndareus.* In the latter, as in *L. minos,* the male stylet has one 180° turn (rather than being spiralized as in *L. castor*). The bursa mouthpiece of *L. minos,* furthermore, is far from being as robust as in *L. castor* and, to a lesser degree, *L. pollux,* but almost as delicate as that of *L. tyndareus.*

The statocyst of *L. minos* confirms not only the remarkable variability in statolith numbers known from other members of the genus (from 2 to 5) but also the mean statolith number which, in all populations that have so far been analyzed, is always somewhat above 3 (3.22 in *L. minos,* 3.11 in *L. castor,* 3.54 in *L. pollux,* and 3.40 in *L. tyndareus*). Only *L. evelinae* is reported to have 2 statoliths, but Marcus' (1950) description is based almost exclusively on preserved and sectioned specimens which may not have revealed such variability.

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NOTES ON LYCHNOPHORINAE FROM MINAS GERAIS, BRAZIL, A SYNOPSIS OF *LYCHNOPHORIOPSIS* SCHULTZ-BIP., AND THE NEW GENERA *ANTEREMANTHUS* AND *MINASIA* (VERNONIEAE: ASTERACEAE)

Harold Robinson

Abstract.—Limits of the Vernonian subtribe Lychnophorinae are refined using pubescence, style bases, anther appendages, and pollen, with an emphasis on the anther appendages. *Episcothamnus* H. Robinson is reduced to synonymy with the formerly monospecific *Lychnophoriopsis* Schultz-Bip. *Lychnophora damazioi* Beauverd and *L. candelabrum* Schultz-Bip. are transferred to *Lychnophoriopsis,* and *L. hatschbachii* is described as new. A key is given to the four species of *Lychnophoriopsis. Anteremanthus hatschbachii* is described as a new genus and species from Minas Gerais, Brazil. The genus *Minasia* is described for *Vernonia alpestris* Baker, *M. scapigera* nom. nov. (for *Vernonia scapigera* Baker hom. illeg.), and *M. pereirae* sp. nov. The 10 genera presently included in the Lychnophorinae are listed. Among the genera excluded from the subtribe are *Chresta* Vell. ex DC. and *Soaresia* Schultz-Bip.

A specimen of Vernonieae from Brazil sent some years ago by Gert Hatschbach has been recognized from the first as an undescribed species, but the generic placement remained undecided until the present study. The specimen shows the general form of the genus *Vernonia* Schreb. s.l, with discrete multiflowered heads and type A pollen. Nevertheless, many features of the plant, such as the large, abruptly petiolate, leathery leaves and the appressed dense pubescence, made assignment to *Vernonia* a repellent idea, even though the proper relationship remained unresolved. A detailed review of characters has now demonstrated a proper place for the specimen in the subtribe Lychnophorinae. Also resolved at the same time are the positions of a number of other Lychnophorinae from the state of Minas Gerais in Brazil, where many members of the subtribe are concentrated.

The Lychnophorinae have been defined in the past mostly by the few-flowered heads in dense glomerules and the often broad, strap-shaped, deciduous inner segments of the pappus. However, within the traditional Lychnophorinae the character of the number of florets in the head fails even in the generic pair *Lychnophora/Lychnophoriopsis,* and the pappus in such genera as *Eremanthus* is sometimes capillary. In addition, the present re-evaluation of characteristics of the subtribe shows that many unusual, robust Vernonieae of eastern Brazil should be considered members of the subtribe Lychnophorinae, in spite of the facts that their heads may have numerous florets and may not be densely congested in clusters, and that their pappus segments may be capillary. The alternative defining characteristics cited here are not necessarily restricted to the Lychnophorinae, but they seem rather consistent within the group. These include a lack of enlarged nodes or sclerified cells at the bases of the styles, usual extensive presence of a pubescence of T-shaped hairs, presence of sclerified cells in the anther appendages, lack of glands on the anther appendages, and presence of Type A pollen (Keeley & Jones 1979) (*Lychnophora*-type of Stix 1960).

Characters most notable in the subtribe Lychnophorinae for their nearly complete absence are sterile tails appended to the basal ends of the fertile anther spurs, glands on the anther appendages, or paleae on the receptacle. Distinct sterile tails on the anther thecae occur in few of the Lychnophorine genera reviewed, although they occur in various Piptocarphinae and many Paleotropical Vernonieae. In the Lychnophorinae, as recognized here, the monotypic *Proteopsis* Mart. & Zucc. ex Schultz-Bip. has distinct sterile tails on the basal ends of the fertile spurs of the anthers, whereas the genus *Minasia* described below has very short tails. Glands have not been seen on the anther appendages in any Lychnophorinae, although glands, or in a few cases such as *Vernonia fuertesii* (Urban) H. Robinson and *V. petiolaris* DC., short spines occur erratically on the anther appendages in various Vernonineae. The receptacle seems to lack distinct paleae in unquestioned Lychnophorinae. Monotypic Brasilian genera that have pales such as *Heterocoma* DC. and *Bishopalea* H. Robinson or that have receptacular projections such as *Sipolisia* Glaziou ex Oliv., and related genera such as *Alcantara* Barroso (Robinson 1981), were placed in the Vernoniinae by Robinson et al. (1980), and have never been placed in the Lychnophorinae. They seem to belong to no presently named subtribe.

Enlargements or sclerified cells at the base of the style are absent from all unquestioned Lychnophorinae. There is a small sclerified node at the base of the style in the monotypic genus *Albertinia* Spreng., placed in the Lychnophorinae by Robinson et al. (1980), but that genus has no character closely associated with the Lychnophorinae in this study except a partially sclerified anther appendage, and it is here excluded from the subtribe. The lack of such a node seems particularly important in view of the wide occurence of such a structure in many Vernoninae and Piptocarphinae.

The sclerified or partially sclerified cells of the anther appendage seem to have special significance in delimiting a number of groups in the tribe including the Lychnophorinae. Members of the subtribe Vernoniinae show little or no sclerification of the cell walls of the anther appendage, and many of the appendages in the group also bear glands or even short hairs. Examples of the subtribe include *Vernonia* and the genera of the *Lepidaploa* Complex (Robinson 1990). In contrast, the cells of the anther appendage have distinctly sclerified walls in all unquestioned members of the Lychnophorinae, and none are known to bear glands. The sclerified cells may be marginal as in *Eremanthus* Less. or throughout the appendage as in *Lychnophora* Mart. Such thickenings are also seen in some other genera mentioned above that may be related to the Lychnophorinae but are presently excluded such as *Heterocoma* and *Bishopalea.* In *Albertinia* they are only weakly developed at the margins. A comparatively unrelated subtribe that seems to characteristically have sclerified appendages is the Piptocarphinae, but the latter usually has a distinct sclerified node at the base of the style (lacking in *Pollalesta* H.B.K.) and has round-tipped sweeping hairs in the style branches. Sweeping hairs of the subtribe Lychnophorinae are like most non-piptocarphine Vernonieae in having pointed tips (Robinson 1980b). The Piptocarphinae is broadened by these characters to include the recently described *Cuatrecasanthus* H. Robinson and *Joseanthus* H. Robinson (1989). Anther appendages with sclerified cells also occur in the Mexican and Mesoamerican *Lepidonia* Blake (Robinson & Funk 1987) which is presently unplaced in any recognized subtribe. Previously placed in the Vernoniinae (Robinson et al. 1980), but here left unplaced subtribally, is the neotropical *Pacourina* Aubl. that has a sclerified anther appendage co-occurring with lophate Type E pollen (Keeley & Jones 1979), a type most common in paleotropical elements of the tribe.

The pollen type of the Lychnophorinae is exclusively Type A, having a weakly lophate surface and a continuous perforated tectum. The type is considered a reversion from more strongly lophate ancestors in the Vernonieae (Robinson 1990), but it is nevertheless one of the most common forms in the tribe and is consistent in many groups such as the Piptocarphinae and typical *Vernonia.* Two genera often placed in the Lychnophorinae that have lophate pollen are *Soaresia* Schultz-Bip. nom. cons. (≡*Bipontia* Blake) and *Chresta* Vell. ex DC. (Robinson 1980a, excluding *Eremanthus eriopus* Schultz-Bip. ex Baker). *Chresta,* including *Argyrovernonia* MacLeish (1984), *Glaziovianthus* Barroso (MacLeish 1985a), and *Pycnocephalum* (Less.) DC. (MacLeish 1985b), was traditionally included in the Lychnophorine *Eremanthus* (Baker 1873), but *Chresta* has non-sclerified anther appendages in addition to the lophate pollen found in most of the species. *Chresta* and *Soaresia* Schultz-Bip., although placed in the subtribe by Robinson et al. (1980), are not considered lychnophorine in the present study.

The Vernonieae have many taxa in both hemispheres bearing T-shaped hairs. Such hairs are particularly prominent in many members of the Lychnophorinae, even commonly occurring on the corolla lobes (Figs. 17, 25).

The Lychnophorinae, as characterized in this study, is extended to clearly include a number of Neotropical species concentrated in Minas Gerais, Brazil that have at times been compared with or questionably included in the genus *Vernonia.* Among the latter are *Lychnophora damazioi* Beauverd, which has recently been transferred to *Vernonia* (Leitão Filho & Semir 1979). It proves to be lychnophorine as Beauverd (1913) originally supposed, and it is placed in the genus *Lychnophoriopsis,* which is revised below. Also included is the Hatschbach specimen for which the study was initiated, and for which a new monospecific genus *Anteremanthus* is described below. Finally, the Lychnophorinae includes the problematic *Vernonia alpestris* Baker, which is here made the type of the new genus *Minasia,* containing three species.

The Lychnophorinae here is considered to include the following ten genera: *Anteremanthus* H. Robinson, *Chronopappus* DC., *Eremanthus* Less. (syn. *Sphaerophora* Schultz-Bip., not Blume, ≡ *Paralychnophora* MacLeish), *Vanillosmopsis* Schultz-Bip, *Lychnophora* Mart. (syn. *Haplostephium* Mart.), *Lychnophoriopsis* Schultz-Bip. (syn. *Episcothamnus* H. Robinson), *Minasia* H. Robinson, *Piptolepis* Schultz-Bip., *Pithecoseris* Mart., *Proteopsis* Mart. & Zucc. ex Schultz-Bip. The precise limits of the tribe, limits of some of the genera, and detailed relationships between the genera remain to be resolved.

Synopsis of *Lychnophoriopsis* Schultz-Bip.

Lychnophoriopsis Schultz-Bip., Pollichia 20/21:375. 1863. Type: *Lychnophoriopsis heterotheca* Schultz-Bip. ≡ *Lychnophora heterotheca* (Schultz-Bip.) Jones & Coile.

Episcothamnus H. Robinson, Phytologia 48: 209. 1981. Type: *Lychnophora candelabrum* Schultz-Bip. ≡ *E. candelabrum* (Schultz-Bip.) H. Robinson.

Plants shrubby, weakly candelabriform, 1–2 m high. Stems and branches 5–10 mm wide, densely whitish tomentose or lanate, hairs with spreading tips. Leaves densely spirally inserted, sessile, oblong to linear, mostly 2–16 cm long and 0.3–0.9 cm wide, base slightly constricted, lateral margins distinctly recurved, sometimes nearly meeting below, apex rounded to narrowly acute; upper surface green, glabrous to sparsely pilose, lower surface whitish lanate with appressed to loose T-shaped hairs; venation pinnate or with secondary veins joining in more or less longitudinal series. Inflorescence densely spiciform; heads discoid, sessile in axils of reduced leaves, contiguous or nearly so, involucre campanulate, 20–25 mm high and mostly 12–15 mm wide; involucral bracts ca. 30–60, subimbricate, of graduated lengths, tips rounded to narrowly lanceolate or shortly aristate, inner bracts sometimes with distinctly narrowed and reflexed tips; outer surfaces densely lanate to sometimes mostly glabrescent; receptacle glabrous, without pales. Florets regular, 9–23 in a head, rarely heteromorphic with inner achenes sterile; corollas lavender, narrowly funnelform, 9–15 mm long, glabrous below, with long narrow tube, throat short and scarcely broadened, linear lobes glanduliferous and hairless or with few to many contorted or T-shaped hairs; thecae without sterile basal appendages on lower ends of spurs, ca. 3–5 mm long; appendages narrowly oblong-ovate to lanceolate, 1–2 mm long, with distinctly weakly sclerified walls throughout, without glands; style base without node or sclerified cells; sweeping hairs of style branches acute-tipped. Achenes 2.5–6.0 mm long, 8–10-ribbed, glabrous, with layers of elongate sclerified cells in walls, with scattered idioblasts on surface sometimes in short series; base truncate with a poorly differentiated carpopodium, with oblong sclerified cells in 4–5 series; pappus biseriate, outer series of long narrow squamae, sometimes basally connate, inner segments weakly persistent or easily deciduous, strap-shaped with few weak marginal teeth or bristle-like distally with scabrae on sides and surfaces, often twisted; in plants with heteromorphic achenes, the inner pappus segments strap-shaped in outer fertile achenes, bristle-like in inner sterile achenes. Pollen grains somewhat oblate, 50–60 μm in diameter in fluid, Type A with perforated tectum continuous over areoles.

The genus is notable for its densely spirally inserted leaves with recurved lateral margins and its heads of 10–25 florets borne in dense, cylindrical, spicate clusters among axils of somewhat shortened terminal leaves. Central sterile achenes with a differentiated pappus were originally used to distinguish the genus from the closely related *Lychnophora* (Schultz-Bip. 1863), but they have not been seen with certainty in any specimens. As a result, the genus *Episcothamnus* (Robinson 1981) is clearly congeneric, and the two type species are very closely related.

The closest generic relationship of *Lychnophoriopsis* is to *Lychnophora,* which has the same type of achenes having distinctive, poorly differentiated carpopodia with elongate cells. The genera could be combined, but the heads of *Lychnophoriopsis* are markedly larger and more discrete than those of *Lychnophora,* and are borne on longer inflorescences. The heads of *Lychnophoriopsis* have distinctly more florets and do not form secondary heads with each other, as in *Lychnophora.* This difference was emphasized by Leitão Filho & Semir (1979) when they removed *L. damazioi* from *Lychnophora.* The other character cited by Leitão Filho and Semir was the more persistent inner pappus of *L. damazioi,* but the pappus in the other species is more deciduous, as in *Lychnophora.* The anther appendages of *Lychnophora* have characteristically stronger thickenings in the cell walls thoroughout the appendage.

Key to the Species of *Lychnophoriopsis*

1. Leaves short with rounded tips; all involucral bracts narrowly lanceolate to linear; inner pappus segments bristle-like, rather persistent, scarcely flattened in distal half, distinctly scabrous outside and on margins .... *L. damazioi*

– Leaves long with acute tips; most involucral bracts ovate or broadly lanceolate; inner pappus segments flattened throughout, easily deciduous, toothed only on margins ... 2

2. Involucral bracts with broadly rounded tips, becoming mostly gla-

brous with age; inflorescence more than twice as long as wide .... *L. hatschbachii*

– Involucral bracts with narrowly obtuse or acute tips, with persistent white tomentum on whole outer surface; inflorescence less than twice as long as wide 3

3. Inflorescence as wide as long; tips of involucral bracts obtusely pointed to shortly acute; heads with 10–17 florets; leaf margins more broadly recurved near base, nearly meeting underneath .... *L. heterotheca*

– Inflorescence longer than wide; tips of involucral bracts narrowly acute; heads with 20–25 florets; leaf margins not more broadly recurved near base, not nearly meeting underneath .... *L. candelabrum*

Lychnophoriopsis candelabrum (Schultz-Bip.) H. Robinson, comb. nov.

Lychnophora candelabrum Schultz-Bip., Pollichia 20/21:345. 1863. Type: Brazil; Minas Gerais, Sello (B, destroyed). Neotype (selected by Robinson 1981): Brazil; Minas Gerais, 62 km SW of Diamantina toward Curvelo, King & Bishop 8573 (UB, isoneotype US).

Episcothamnus candelabrum (Schultz-Bip.) H. Robinson, Phytologia 48:210. 1981.

The epithet is treated as a noun in apposition and is not declined. The species is known at this time only from the neotype. Other material recently identified as this species has been redetermined in this study as *L. heterotheca.* The two species are very close, but *L. candelabrum* is generally more robust; detailed distinctions are given under *L. heterotheca.*

Lychnophoriopsis damazioi (Beauverd) H. Robinson, comb. nov.

Lychnophora damazioi Beauverd, Bull. Soc. Bot. Genève, series II, 5:241. 1913. Type: Brazil; Minas Gerais, Serra do Cipó, in campis, June 1908, Damazio 2010 (G).

Vernonia damazioi (Beauv.) Leitão Filho & Semir, Revista Brasil. Bot. 2:113. 1979.

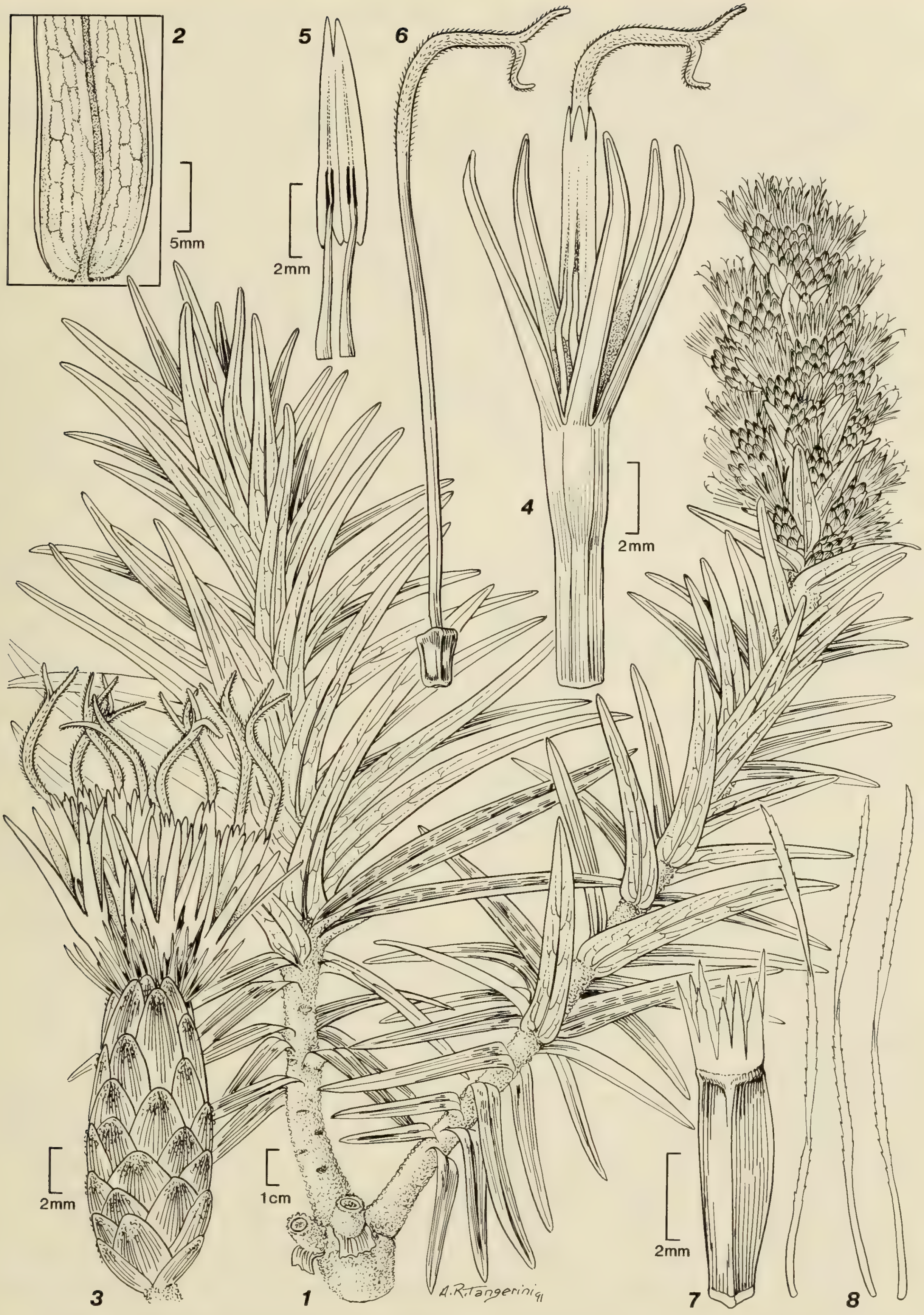
Lychnophora unicaulis Glaziou, Bull. Soc. Bot. France 56, Mém. 1(3):379. 1909, nom. nud.

The species is the most distinctive in the genus in its short blunt leaves and narrow, scabrous, rather persistent pappus bristles. The involucral bracts have the longest and narrowest tips of any member of the genus, distinctly narrower than those of *L. candelabrum.*

Lychnophoriopsis hatschbachii H. Robinson, sp. nov.
(Figs. 1–8)

Plantae fruticosae pauce ramosae ad 1.5 m altae. Folia dense spiraliter inserta sessilia lineari-lanceolata plerumque 5–10 cm longa base 7–10 mm lata margine anguste recurvata apice acuta supra glabra subtus appresse albo-lanata, nervulis aliquantum longitudinaliter dispositis. Inflorescentiae elongatae ad 10 cm longae et ca. 5 cm latae. Capitula ca. 3 cm longa et 0.8–1.0 cm lata; bracteae involucri ca. 27–30 appresse subimbricatae 4–17 mm longae et ca. 3 mm latae apice rotundatae vel obtusae extus plerumque glabrae vel glabrescentes distaliter persistentiter dense glanduliferae et arachnoideo-tomentellae. Flores ca. 9–10 in capitulo; corollae lavandulae ca. 15 mm longae plerumque glabrae in lobis perpauce glanduliferae non piliferae, tubis ca. 5 mm longis, faucibus ca. 2 mm longis, lobis ca. 7 mm longis; thecae ca. 5 mm longae; appendices lanceolatae ca. 2 mm longae. Achaenia ca. 5 mm longa glabra; squamae pappi exteriores 1.5–2.0 mm longae, setae interiores taeniatae ca. 7 mm longae vix vel non contortae.

Type: Brazil; Minas Gerais, Mun. Diamantina, Rod. Guinda-Cons. Mata, km 20, campo rupestre, solo rochoso, 1000 m, arbusto pouco ramificado, até 1.5 m, capítulos



Figs. 1–8. *Lychnophoriopsis hatschbachii* H. Robinson; 1. Habit; 2. Underside of leaf base showing venation; 3. Head, moist; 4. Corolla with anthers and style; 5. Anthers; 6. Style with nectary at base; 7. Achene showing outer pappus segments; 8. Segments of deciduous inner pappus.

lilás, Hatschbach & Nicolack 53058 (MBM; isotype US).

Paratype: Brazil; Minas Gerais, s.l., s.d., Glaziou 20372 (K).

The paratype collection of the species for some years served the author as a model for the type species of the genus, *Lychnophoriopsis heterotheca.* The present study has shown it represented a throughly distinct undescribed species. The more elongate inflorescences and blunt involucral bracts with more nearly glabrous outer surfaces easily distinguish the species. The leaves also have much more appressed pubescence on the under surface and the venation is more nearly longitudinal in appearance than in other species of the genus.

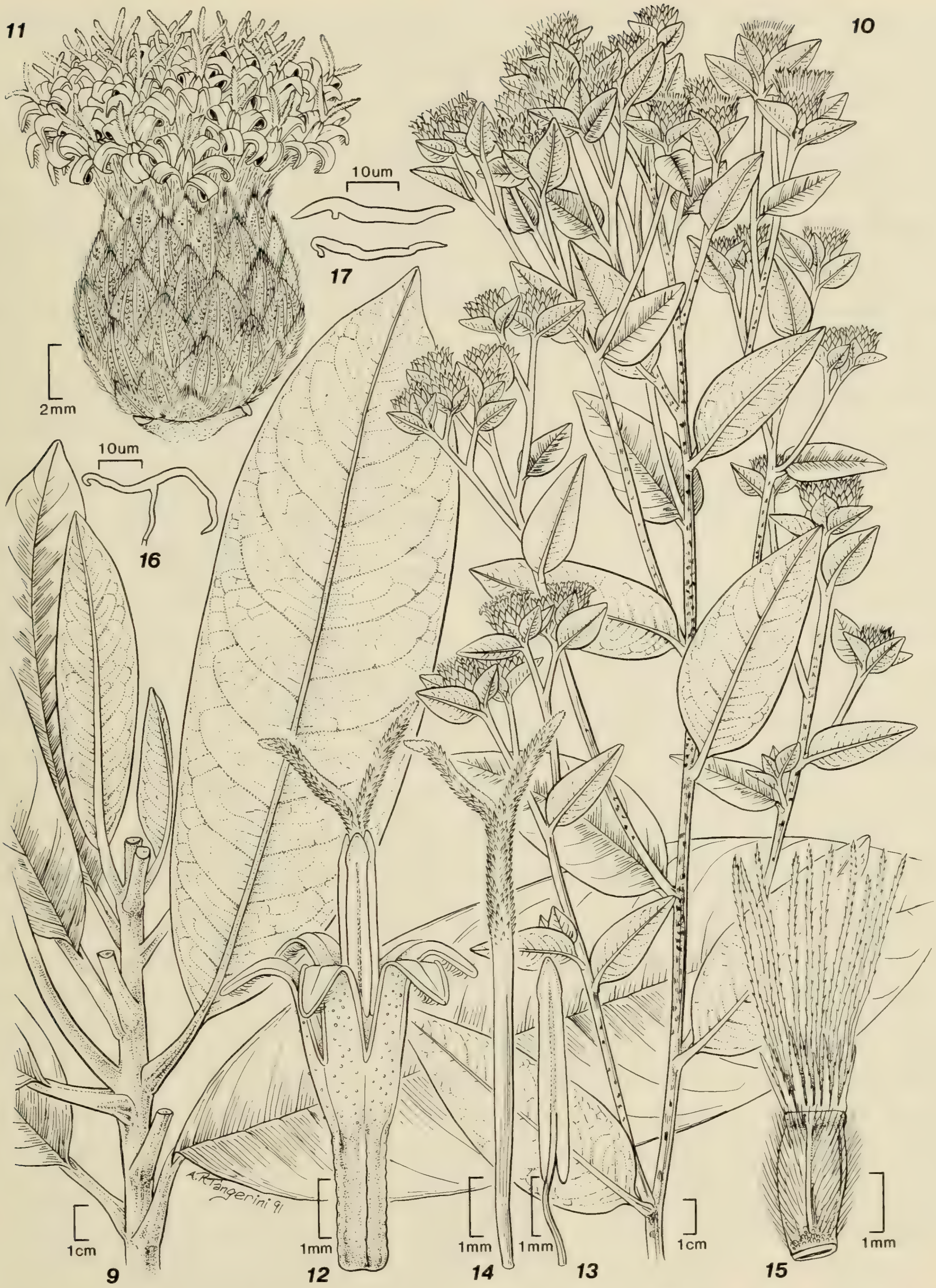
Lychnophoriopsis heterotheca Schultz-Bip., Pollichia 20/21:376. 1863. Type: Brazil; Minas Gerais, s.l., s.d., Reidel 1009 (P).

Examination of a photograph of the type shows the species is not the same as the Glaziou herbarium specimen at Kew under the name *L. heterotheca* identified above as *L. hatschbachii.* The species is actually much closer to *L. candelabrum,* which was originally described at the same time (Schultz-Bip. 1863), and specimens other than the neotype recently identified as *L. candelabrum* prove to be the present species. The two species are close, but seem to show consistent differences in shape of the leaf base, length versus width of the inflorescence, size of the heads, shape of tips of the involucral bracts, and number of florets in the heads.

Additional specimens seen: Brazil; Minas Gerais, Serra do Espinahaço, 67 km SW of Diamantina on hwy BR-259, Ferreira, Stutts, MacLeisch & Smith 998 (US); Mun. Gouveia, Corrego do Tigre, 1100 m, Hatschbach 27245 (US); Mun, Gouveia, subida da Serra do Espinhaço, Rod. BR-259, Hatschbach 44653 (US); Serra do Espinhaço, BR-259, Hatschbach, Anderson, Barneby & Gates 36435 (F, K, NY, US, VEC, VEN); Mun. Gouveia, Barro Preto, Torre da Telemig, Hatschbach & Kummrow 49697 (US); Mun. Gouveia, prox. trevo para Datas, Rod. BR-259, Hatschbach & Nicolack 53096 (NY).

Anteremanthus hatschbachii H. Robinson, gen. et sp. nov.
(Figs. 9–17)

Plantae fruticosae ad 2 m altae, pilis plerumque T-formibus. Caules irregulariter angulati vel sulcati dense appresse tomentosi non fistulosi. Folia alterna, petiolis distinctis 0.5–2.7 cm longis crassis sulcatis appresse tomentosis; laminae coriaceae oblongo-ellipticae plerumque 9–23 cm longae 2.5–8.0 cm latae base rotundatae vel breviter obtusae margine integrae apice breviter acutae supra virides minute appresse pilosulae subtus albescentes dense appresse tomentosae, nervis secundariis pinnatis numerosis. Inflorescentiae thyrsoideae, ramis alternis longis valde ascendentibus appresse tomentellis in partibus nigromaculatis, ramulis distalibus plerumque 0.5–1.8 cm longis, bracteis primariis foliiformibus breviter petiolatis 4–8 cm longis 1.8–2.8 cm latis in laminis oblongo-ovatis, bractiis secundariis subsessilibus 3.0–1.5 cm longis 0.8–1.2 cm latis, bracteis capitulorum basilaribus foliiformibus breviter ovatis plerumque 0.5–1.5 cm longis. Capitula late campanulata 10-12 mm alta et lata; bracteae involucri ca. 60 subimbricatae ca. 5 seriatae ovatae vel oblongo-ovatae 3–7 mm longae inferne ca. 2 mm latae apice acutae vel apiculatae extus dense minute glandulo-punctatae plerumque T-formiter arachnoideo-pilosulae; paleae nullae. Flores ca. 60 in capitulo, corollae albae ca. 5 mm longae, tubis ca. 1 mm longis, faucibus ca. 1 mm longis, lobis ca. 3 mm longis et 0.5 mm latis extus dense glanduliferis et pilosulis, pilis plerumque non T-formibus; thecae antherarum 3.0–3.5 mm longae; appendices antherarum triangulares ca. 0.6 mm longae et 0.35 mm latae, parietibus in cellulis marginalibus mediocriter incrassatis; basi stylorum non noduliferi non scleroidei. Achaenia ca. 3 mm longa 8–10-costata, dense longe setulifera base dense glanduli-



Figs. 9–17. *Anteremanthus hatschbachii* H. Robinson; 9. Section of vegetative stem; 10. Inflorescence; 11. Head, moist; 12. Corolla with anthers and style; 13. Anther; 14. Style; 15. Achene; 16. Trichome from lower leaf surface; 17. Trichomes from corolla lobe.

fera plerumque in costis in idioblastis bicellularibus sparsis obtecta; carpopodia annuliformia, cellulis subquadratis ca. 6-seriatis valde scleroideis; setae pappi ca. 40 in parte longiores facile deciduae 5–6 mm longae apice distincte latiores valde armatae, setae pappi in parte intermediores subpersistentes plerumque 3–6 mm longae apice non latiores, setae in seriebus breviores exteriores persistentes ca. 1 mm longae. Grana pollinis in diametro ca. 45 μm in typis A-formibus irregulariter subareolatis.

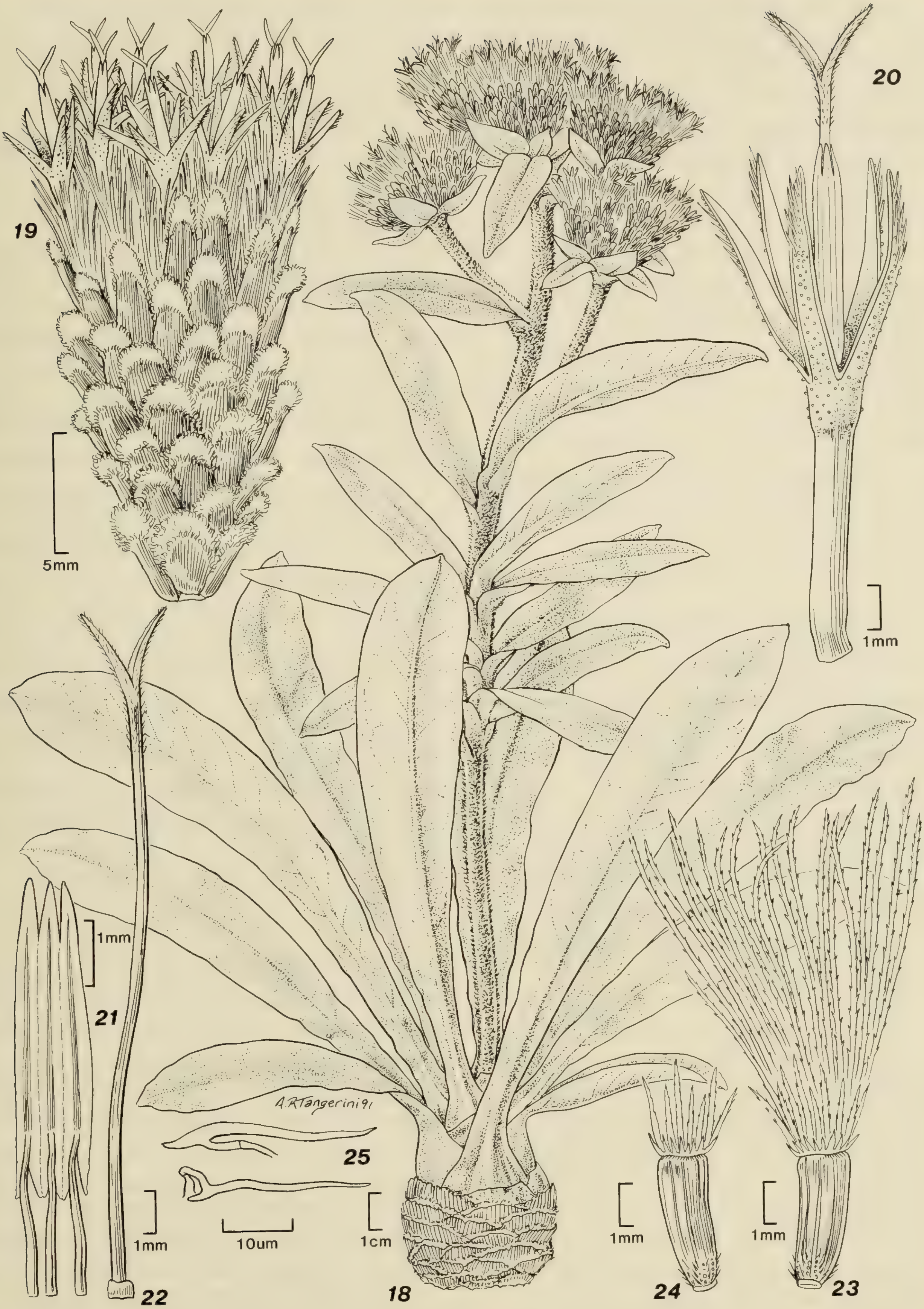
Type: Brazil; Minas Gerais, Mun. Grão Mogol, Rio Itacambiruçu, Campo rupestre, solo rochoso, arbusto 2 m, flores alvas, 15 May 1988, G. Hatschbach & M. Hatschbach & O. S. Ribas 52026 (MBM; isotype US).

The genus is named for the apparently related genus *Eremanthus* Less. with a negative prefix to reflect the strong differences in all the traditional characters. The species is named for the collector Gert Hatschbach of the Museo Botânico Municipal of Curitiba in Paraná.

In vegetative form and in the anther appendage the new genus resembles such species as *Eremanthus bicolor* (Schultz-Bip.) Baker, *E. glomerulatus* Less., and *E. incana* (Less.) Less. The discolorous petiolate leaves and the inflorescence bracts resemble those of *E. bicolor* particularly closely. The branching form of the inflorescence with discrete multi-flowered heads and the elongate funnelform corollas are completely different from any *Eremanthus* and the inflorescence seems almost unique in the Lychnophorinae. The slight approach to the inflorescence type in the subtribe is seen in the most lax types of inflorescence in the following new genus.

Minasia H. Robinson, gen. nov.
(Figs. 18–25)

Plantae herbaceae perennes ad 0.7 m altae, pilis plerumque T-formibus. Caules primarii breves usque ad 4 cm alti perdense foliati. Folia primaria spiraliter inserta superne rosulata sessilia oblanceolata vel lineari-lanceolata 15–20 cm longa et 1–5 cm lata base breviter late amplexicaulia supra basem attenuate late petioliformia margine integra apice breviter acuta supra et subtus dense appresse tomentosa, nervis secundariis ascendentiter pinnatis utrinque ca. 10. Inflorescentiae scaposae numerosae in caulibus secundariis elongatae ad 0.6 m altae velutinae superne interdum ramosae; bracteae foliiformes decrescentes plerumque remotae plerumque 4–8 cm longae 0.5–2.5 cm latae base anguste petioliformes apice distincte acutae vel acuminatae; bracteae superiore congestae. Capitula solitaria in axillis bracteorum superiorum congestorum disposita late campanulata 1.5–2.3 cm alta et 0.7–1.0 cm lata; bracteae involucri 50–60 subimbricatae ca. 5-seriatae oblongae ad 10 mm longae et 2 mm latae apice obtusae vel acutae extus superne dense glanduliferae et tomentosae; paleae nullae. Flores 20–30 in capitulo; corollae lavandulae ca. 8–14 mm longae inferne glabrae vel sparse glanduliferae, tubis 3–5 mm longis, faucibus cylindricis 1.0–1.5 mm longis, lobis 3–6 mm longis extus superne glanduliferae et pauce vel dense piliferae, pilis saepe T-formibus; thecae antherarum 3–4 m longae base breviter appendiculatae; appendices apicales antherarum ovato-oblongae vel lanceolatae 0.25–0.50 mm longae et ca. 0.10–0.12 mm latae, parietibus in cellulis marginalibus mediocriter incrassatis; basi stylorum non noduliferi non scleroidei. Achaenia 2.5–3.5 mm longa ca. 8-costata evanescentiter persparse setulifera in idioblastis pauci-cellularibis sparse obtecta; carpopodia annuliformia, cellulis minute subquadratae ca. 6-seriatis mediocriter scleroideis; setae pappi capillares scabrae mediocriter facile deciduae exteriores breviores ca. 20 attenuatae, setae interiores ca. 35 plerumque 5–9 mm longae apice lateriores. Grana pollinis in diametro ca. 55 μm in typus A-formibus irregulariter subareolatis.



Figs. 18–25. *Minasia alpestris* (Gardner) H. Robinson; 18. Habit; 19. Head; 20. Corolla with anthers and style; 21. Anthers; 22. Style with nectary; 23. Achene with complete pappus; 24. Achene without inner pappus; 25. Trichomes from corolla lobe.

Type: *Vernonia alpestris* Gardner ≡ *Minasia alpestris* (Gardner) H. Robinson.

The two previously known species of the genus have evidently impressed others as being misplaced in *Vernonia.* Jones (1979) did not include the species in his review of *Vernonia* in the New World, although no alternate disposition was indicated. *Minasia* is distinct in its short stemmed, rosulate form with broadened leaf bases encircling much of the stem. The leaves have broadly petioliform bases instead of distinct petioles, as seen in *Anteremanthus,* and the T-shaped hairs form a dense appressed tomentum covering both surfaces. The anthers are different from most in the subtribe by their short but usually distinct, sterile tails.

Key to the Species of *Minasia*

1. Primary leaves linear, with acute apices; inflorescences with heads densely congested in subspherical clusters; achenes with numerous setulae in basal half .... *M. scapigera*
– Primary leaves oblanceolate, with obtuse or shortly acute apices; inflorescences with heads staggered in axils of congested upper bracts; achenes with few setulae below or setulose throughout 2
2. Base of plant 2.0–2.5 cm wide; leaves 12–22 cm long, 2.5–4.5 cm wide; scapes densely velutinous with short spreading hairs; anther appendages ca. 0.5 mm long, ca. 4 times as long as wide, acute; achenes with few setulae below .... *M. alpestris*
– Base of plant 1.0–1.5 cm wide; leaves mostly 5–8 cm long, 0.5–1.0 cm wide; scapes with appressed tomentum; anther appendages ca. 0.25 mm long, ca. 2 times as long as wide, obtuse to subacute; achenes with numerous setulae over whole surface .... *M. pereirae*

Minasia alpestris (Gardner) H. Robinson, comb. nov.
(Fig. 18–25)

Chresta alpestris Gardner, London J. Bot. 1:239. 1842. Type: Brazil; Minas Gerais, Adamantium, in montibus altis et rupestribus Gardner 4820 (BM; isotypes C, photo, K, photo).

Vernonia alpestris (Gardner) Baker, Fl. Bras. 6(2):55. 1873.

The heads of the species seem characteristically larger as well as more loosely disposed than those of *M. scapigera.*

Additional specimens seen: Brazil; Minas Gerais, Mun. Datas, Vargens dos Bastos, 5 km 0, campo rupestre, afloramentos rochosos, capitulos, lilas palido, 13 Sep 1985, Hatschbach & Kummrow 49645 (US); ca. 18 km E of Diamantina, 1100 m, rocky summits with soil-filled crevices and small areas of white sand, herb to ca. 50 cm tall, 19 Mar 1970, Irwin, Fonsêca, Souza, Reis dos Santos & Ramos 27909 (NY, US); just west of Serra, road from Concepcão to Diamantina, occasional on sandstone, herbaceous perennial to 5 dm high, flowers purple, 9 Aug 1960, Maguire, Magalhaes & Maguire 49133 (NY, US).

Minasia pereirae H. Robinson, sp. nov.

Plantae herbaceae rosulatae ad 1.5–2.5 dm altae; caules 1.0–1.5 cm alti in basibus foliorum dense obtecti. Folia anguste oblanceolata plerumque 5–8 cm longa 0.5–1.0 cm lata base breviter amplexicaulia ad 7 mm lata inferne subpetioliformia ca. 2 mm lata apice breviter obtusa vel breviter acuta supra et subtus dense appresse T-formiter pilosa supra appressiores subtus densiores et pallidiores, nervis secundariis obscuris ca. 10 erecto-patentibus brevibus. Inflorescentiae scaposae 1.5–2.5 dm altae; scapi appresse tomentosae inferne sparse et remote bracteiferae, bracteis anguste ellipticis 1–2 cm longis 2–3 mm latis, inflorescentiae superne plerumque aliquantum seriate tricapitatae. Capitula ca. 1 cm alta et lata; bracteae involucri 40–45 ca. 6-seriatae oblongae 1.5–7.0 mm longae 1.0–1.5 mm latae apice obtusae extus dense sordide tomentosae; receptacula alveolata sparse pilosula. Flores ca. 40 in capitulo; corollae lavandulae ca. 8 mm longae, tubis ca. 4 mm longis anguste infundibulares base et superne sparse glanduliferis, faucibus ca. 1.5 mm longis extus glanduliferis, lobis lanceolatis ca. 2.5 mm longis et base 0.6 mm latis extus glanduliferis superne dense contorte vel T-formiter pilosis; thecae antherarum ca. 2 mm longae, appendices apicales antherarum ovato-oblongae ca. 0.25 mm longae et 0.11 mm latae apice obtusae. Achaenia ca. 3 mm longa omnino setulifera; setae pappi pallide rufescentes longiores 5–6 mm longae apice vix angustiores, setae exteriores breviores 1.5–3.0 mm longae apice attentuatae. Grana pollinis in diametro ca. 50 μm.

Type: Brazil; Minas Gerais, Diamantina, Rio das Pedras, flores lilaz, 29 May 1955, Pereira 1626 (NY).

Minasia pereirae has the general habit of *M. alpestris,* but is distinctly smaller in all its parts. In addition to the difference in size, the anther appendages are much shorter in comparison to their length and have blunter tips, and the achenes have setulae throughout their length instead of having them restricted to the basal part.

One other specimen, Brasil: Minas Gerais; Mun. Gouveia, Barro Preto, torre Telemig, campo rupestre, solo rochoso, 20 Mar 1987, Hatschbach, Cervi & Cordeiro 51160 (US); seems to belong to the genus, and it was tentatively determined by the author a few years ago as *Vernonia alpestris.* The mostly appressed pubescence of the stems, head size, corolla length, anther appendage, and achene setulae are most like the present species, but the vegetative parts that are available are mostly different. The specimen consists of slender leafy shoots with a few small densely congested heads distally. The shoots may have arisen from a basal rosette, but a rosette is not present. The leaves are narrowly petiolate, the bases are narrowly inserted on the stem, and the apices are narrowly acute. The pieces cannot be placed with confidence in any of the three species presently recognized in the genus. Further collecting may clarify the relationship of the specimen.

Minasia scapigera H. Robinson, nom. nov.

Vernonia scapigera Baker, Fl. Bras. 6(2):55. 1873, non *Vernonia scapigera* Less., Linnaea 4:250–251. 1829. Type: Brazil; Minas Gerais, Inter Villa de Campanha et St. João d'El Rey, in pratis alpestribus, s.d., Martius s.n. (M, photos NY, US).

The species has long been recognized under the name *Vernonia scapigera* Baker, a later homonym. The species is properly validated here for the first time based on the Baker (1873) description.

Additional specimens seen: Brazil; Minas Gerais, s.l., s.d., Glaziou 19545 (NY); Serra do Espinhaço, ca. 10 km N of São João da Chapada, road to Inhaí, cerrado, gallery and campo, 22 Mar 1970, Irwin, Fonsêca, Souza, Reis dos Santos & Ramos 28085a (US), 28086 (NY); Mun. Pres. Kubitchek, Rod. BR-259, campo rupestre, solo arenoso, capítulos lilás, 1000 m, Hatschbach & Nicolack 53104 (MBM, US); Diamantina, Agua Limpa, flores lilaz, 22 May 1955, Pereira 1459 (NY).

Acknowledgment

The drawings of the three genera were prepared by Alice Tangerini of the Department of Botany, National Museum of Natural History, Smithsonian Institution.

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PROC. BIOL. SOC. WASH.
105(3), 1992, pp. 653–654

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% The Natural History Museum
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Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 26 March 1992 in Vol. 49, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these Applications is invited for publication in the *Bulletin,* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2251 *Bucephalus* Baer, 1827 and *B. polymorphus* Baer, 1827 (Trematoda): proposed conservation in their accepted usage.
2247 *Balea* Gray, 1824 (Mollusca, Gastropoda): proposed conservation.
2634 *Xeromunda* Monterosato, 1892 (Mollusca, Gastropoda): proposed designation of *Helix candiota* Mousson, 1854 as the type species.
2798 *Lincus* Stål, 1867 (Insecta, Heteroptera): proposed conservation, and *L. croupius* Rolston, 1983: proposed conservation of the specific name.
2764 *Acrolocha* Thomson, 1858 (Insecta, Coleoptera): proposed conservation, and *Coprophilus* Latreille, 1829: proposed designation of *Staphylinus striatulus* Fabricius, 1792 as the type species.
2782 *Carabus mollis* Marsham, 1802 (currently *Calathus mollis*; Insecta, Coleoptera): proposed conservation of the specific name.
2796 *Helophorus* Fabricius, 1775 (Insecta, Coleoptera): proposed conservation as the correct original spelling.
2776 *Meladema* Laporte, 1835 (Insecta, Coleoptera): proposed conservation.
2733 *Mycetoporus* Mannerheim, 1831 (Insecta, Coleoptera): proposed designation of *Tachinus punctus* Gravenhorst, 1806 as the type species; proposed conservation of *Ischnosoma* Stephens, 1829; and proposed precedence of *Mycetoporus* over *Ischnosoma.*
2760 *Rhipidocystis* Jaekel, 1901 (Echinodermata, Eocrinoidea): proposed designation of *R. baltica* Jaekel, 1901 as the type species.
2815 *Graptolithus clintonensis* (currently *Monograptus clintonensis*; Graptolithina): proposed attribution to Hall, 1852, and designation of a lectotype.
2826 *Monograptus crenulatus* (currently *Monoclimacis crenulata*; Graptolithina): proposed attribution of the specific name to Elles & Wood, 1911, and proposed designation of a lectotype.
2797 *Scylliorhinus atlanticus* Koefoed, 1927 (currently *Apristurus atlanticus*; Chondrichthyes, Carcharhiniformes): proposed conservation of the specific name.
2807 *Dinodontosaurus* Romer, 1943 (Reptilia, Synapsida): proposed conservation.

2785 *Palaeopropithecus ingens* G. Grandidier, 1899 (Mammalia, Primates): proposed conservation of both generic and specific names.

2770 *Hylobates entelloides* I. Geoffroy Saint-Hilaire, 1842 (Mammalia, Primates): proposed conservation of the specific name.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 26 March 1992 in Vol. 49, Part 1 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1662 *Limax fibratus* Martyn, 1784 and *Nerita hebraea* Martyn, 1786 (currently *Placostylus fibratus* and *Natica hebraea*; Mollusca, Gastropoda): specific names conserved; and *Placostylus* Beck, 1837: *L. fibratus* designated as the type species.

1663 *Fryeria* Gray, 1853 and *F. rueppelii* Bergh, 1869 (Mollusca, Gastropoda): conserved.

1664 RISSOIDAE Gray, 1847 (Mollusca, Gastropoda): given precedence over TRUNCATELLIDAE Gray, 1840.

1665 *Potamilus* Rafinesque, 1818 (Mollusca, Bivalvia): not suppressed.

1666 *Aphrodita imbricata* Linnaeus, 1767 (currently *Harmothoe imbricata*) and *Aphrodita minuta* Fabricius, 1780 (currently *Pholoe minuta*) (Annelida, Polychaeta): specific names conserved.

1667 *Thalassochernes* Beier, 1940 (Arachnida, Pseudoscorpionida): *Chelifer taierensis* With, 1907 designated as the type species.

1668 *Bathynomus* A. Milne Edwards, 1879 (Crustacea, Isopoda): given precedence over *Palaega* Woodward, 1870.

1669 *Dalla* Mabille, 1904 (Insecta, Lepidoptera): conserved.

1670 *Calliphora vicina* Robineau-Desvoidy, 1830 (Insecta, Diptera): specific name conserved.

1671 *Strophomena* de Blainville, 1824 (Brachiopoda): *Leptaena planumbona* Hall, 1847 designated as the type species.

1672 *Muraena* Linnaeus, 1758 and *Anguilla* Schrank, 1798 (Osteichthyes, Anguilliformes): placed on the Official List of Generic Names.

1673 LIPARIDAE Gill, 1861 (Osteichthyes, Scorpaeniformes): spelling confirmed.

1674 THRESKIORNITHIDAE Poche, 1904 (Aves, Ciconiiformes): given precedence over PLATALEIDAE Bonaparte, 1838 and EUDOCIMIDAE Bonaparte, 1854.

PROC. BIOL. SOC. WASH.
105(3), 1992, p. 655

BIOLOGICAL SOCIETY OF WASHINGTON

119th Annual Meeting, 19 May 1992

The meeting was called to order by Leslie Knapp, President, at 10:00 AM in the Waldo Schmitt Room, National Museum of Natural History.

Les summarized events leading to a three-year contract with Allen Press to handle dues, subscriptions and the membership list. The cost of this contract is $5/subscriber, and it can be cancelled at any time with three months notice.

Les announced the election results. The new elected officers and council members are listed on the inside front cover of this issue.

Mike Vecchione, Treasurer, presented his report. Total income for the period of 22 May 1991–18 May 1992 was $83,528, and total expenditures were $85,149. Expenditures included $5,487 for purchase of a computer for the Treasurer and a computer and printer for the Editor.

Brian Robbins, Editor, then presented his report. The four issues of Volume 104 of the *Proceedings* were published on 13 March, 18 June, 25 September, and 18 December 1992, containing a total of 81 papers and 905 pages. This is the lowest number of papers published in four years, but it should increase to 90–100 next year. There were 101 submissions in 1991, up from 87 in 1990, and as of 1 May 1992, submissions were running ahead of the totals for the same periods in 1989–1991. There is no current backlog. Brian noted that Steve Cairns resigned as Associate Editor and was replaced by Jon Norenburg.

Austin Willims, Back-issues Custodian, reported that with reorganization, there is now storage space for 4–5 years of back issues.

Frank Ferrari presented the Report of the Membership Committee Membership in the society peaked at 652 in 1987, subscriptions peaked at 253 in 1984, and memberships plus subscriptions peaked in 1986. As of December 1990, membership was down 2.5% and subscriptions were down 4.7%. The Membership Committee recommends that the Treasurer be encouraged to provide a complete report of membership and subscriptions for each fiscal year, and that the society develop a strategy for a membership drive to be followed after 1–2 years with a subscription drive.

Storrs Olson and Ellis Yochelson suggested that the society consider doing something special in honor of the upcoming 150th Anniversary of the Smithsonian Institution in 1996.

A motion was made and seconded that the meeting be adjourned; Les adjourned the meeting at 10:30 AM.

Respectfully submitted,
G. David Johnson
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

A plea for adequate citation of authors of taxa in systematic studies
Douglas A. Kelt and R. Eduardo Palma 411

A new subspecies of *Chamaea fasciata* (Wrentit) from Oregon (Aves: Timaliinae)
M. Ralph Browning 414

The generic name for Crested Caracaras (Aves: Falconidae)
Richard C. Banks and Carla J. Dove 420

A new Chinese eyed turtle of the genus *Sacalia* (Batagurinae: Testudines)
John B. Iverson and William P. McCord 426

A new subspecies of *Cuora galbinifrons* (Testudines: Batagurinae) from Hainan Island, China
John B. Iverson and William P. McCord 433

A new *Lepidodactylus* (Reptilia: Gekkonidae) from Guadalcanal Island, Solomons
Walter C. Brown, Michael McCoy, and Gordon H. Rodda 440

Two new snappers (Teleostei: Lutjanidae: Apsilinae): *Paracaesio paragrapsimodon* Anderson and Kailola from the western Pacific and *P. waltervadi* Anderson and Collette from the western Indian Ocean
William D. Anderson, Jr., Patricia J. Kailola, and Bruce B. Collette 443

A new species of *Sphoeroides* pufferfish (Teleostei: Tetraodontidae) with extensive hyperostosis from the Pliocene of North Carolina
James C. Tyler, Robert W. Purdy, and Karl H. Oliver 462

Phyllophorus (*Urodemella*) *arenicola*, a new sublittoral sea cucumber from the southeastern United States (Echinodermata: Holothuroidea) David L. Pawson and John E. Miller 483

The immature stages of *Atherigona orientalis* Schiner (Diptera: Muscidae)
Márcia Souto Couri and Paulo Francisco de Araújo 490

Studies of Neotropical caddisflies, XLIX: The taxonomy and relationship of the genus *Eosericostoma*, with descriptions of the immature stages (Trichoptera: Helicophidae)
Oliver S. Flint, Jr. 494

Designation of lectotypes for the species of *Munida* (Crustacea: Anomura: Galatheidae) collected by the U.S. Coast Survey Steamer *Blake* (1877–1879) and the description of a new species Gustavo Augusto S. de Melo-Filho and Gustavo Augusto S. de Melo 512

Larval development of the Golden Crab, *Chaceon fenneri* (Manning & Holthuis, 1984) (Decapoda: Brachyura: Geryonidae), reared in the laboratory
Kenneth C. Stuck, Harriet M. Perry, Lidia M. Stuck, and Adeline A. Barrett 521

New species of fresh-water crabs of the genus *Neostrengeria* (Crustacea: Decapoda: Pseudothelphusidae) from Colombia Martha R. Campos 540

A new Cretaceous crab, *Diaulax millerae* (Crustacea: Decapoda), from the Northern Atlantic Coastal Plain, U.S.A. Gale A. Bishop 555

Redescription of the hippolytid shrimp *Trachycaris rugosa* (Bate) (Crustacea: Decapoda: Caridea) from the western Atlantic, with notes on sexual dimorphism Maria M. Criales 562

A new genus for *Corallianassa xutha* Manning (Crustacea: Decapoda: Callianassidae)
Raymond B. Manning 571

Description of the mature female and epicaridium larva of *Cabirops montereyensis* Sassaman from southern California (Crustacea: Isopoda: Cabiropidae) Clay Sassaman 575

A new species of *Coralliodrilus* (Oligochaeta: Tubificidae) from the eastern Gulf of Mexico, and a new record of *C. corpulentus* from South Carolina
Christer Erséus and Michael R. Milligan 585

Phyllodocids (Annelida: Polychaeta) of Belize, with the description of three new species
Danny Eibye-Jacobsen 589

Two new genera and four new combinations of Sigalionidae (Polychaeta)
Marian M. Pettibone 614

Pseudopolydora diopatra, a new species (Polychaeta: Spionidae) from Taiwan
Hwey-Lian Hsieh 630

Lurus minos, the first species of Luridae (Turbellaria: Rhabdocoela) from the Old World
Wolfgang Sterrer 636

Notes on Lychnophorinae from Minas Gerais, Brazil, a synopsis of *Lychnophoriopsis* Schultz-Bip., and the new genera *Anteremanthus* and *Minasia* (Vernonieae: Asteraceae)
Harold Robinson 640

International Commission on Zoological Nomenclature: Applications and Opinions 653

Biological Society of Washington: 119th Annual Meeting 655

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TWO NEW SPECIES OF *CHRYSOLAENA* FROM BRAZIL (VERNONIEAE: ASTERACEAE)

Harold Robinson

Abstract.—*Chrysolaena hatschbachii* and *C. nicolackii* are described from southern Brazil. The new species differ from other members of *Chrysolaena* and approach *Lepidaploa* by the basal sclerified ring on the style. Inflorescence form, stem and leaf pubescence, glanduliferous anther appendages, pollen structure, and details of the style base confirm the generic placement and show that the two new species are not more closely related to *Lepidaploa* than are other species of *Chrysolaena*. A key is provided for the nine species of *Chrysolaena*.

The genus *Chrysolaena* was described by Robinson (1988b) as a segregate from *Vernonia* Schreb. in one of a series of studies of the *Lepidaploa* Complex (Robinson 1987a, 1987b, 1987c, 1988a, 1988c, 1990). Included were seven species with rather uniform appearance in sericeous pubescence, inflorescences with seriate-cymose branches and sessile non-apical heads, anther appendages with glands, Type C pollen (Jones 1979) and non-sclerified style bases. The new species described below have most of the basic characteristics of the genus, but have a distinct annulus of sclerified cells at the base of the style, a feature approaching the condition found in the related genus *Lepidaploa* (Cass.) Cass.

Chrysolaena was originally established to include *C. flexuosa* (Sims) H. Robinson, *C. herbacea* (Vell.) H. Robinson, *C. lithospermifolia* (Hieron.) H. Robinson, *C. platensis* (Spreng.) H. Robinson, *C. propinqua* (Hieron.) H. Robinson, and *C. verbascifolia* (Less.) H. Robinson, species that were the larger part of what Jones (1981) had called *Vernonia* series *Flexuosae*, plus an additional species, *C. oligophylla* (Vell.) H. Robinson (including *Vernonia hypochlora* Malme). All the species have Type C lophate pollen with areoles at the poles and baculae weakly attached to the foot layer (Robinson 1988b, figs. 1, 2) and are sericeous or velutinous to sublanate on the stems, leaves and involucre. The concept was reinforced by the lack of sclerified cells at the base of the style and the usual presence of glands on the anther appendages, both characters useful to distinguish *Chrysolaena* from the related genus *Lepidaploa*.

The two new species from Paraná, Brazil were first noticed in material recently sent for identification by Dr. Gert Hatschbach of the Museo Botânico Municipal in Curitiba. Two additional specimens were subsequently found misdetermined in folders of more common members of *Chrysolaena*. The two species were distinct from other *Chrysolaena* species in their generally more robust form, broad heads, and somewhat reflexed tips on their subequal involucral bracts. Microscopic examination showed the pollen and glanduliferous anther appendages of *Chrysolaena*, but also revealed a narrow ring of sclerified cells at the base of the style. The latter character distinguishes the two species from other members of *Chrysolaena* and could indicate some relationship to *Lepidaploa*, where the characteristic is well developed. The glanduliferous anther appendage is also an imperfect distinction between the genera, for *C. herbacea* often lacks the glands and two species of *Lepidaploa*, *L. helophila* (Mart. ex DC.) H. Robinson (Robinson 1990) and many Central

American specimens of *L. canescens* (H.B.K.) H. Robinson have some glands on the appendages.

The distinctions between *Chrysolaena* and *Lepidaploa* may seem to be weakened by the presence of the sclerified style base in the two new species; nevertheless, a careful review of all characters places both species fully within *Chrysolaena* and completely outside of *Lepidaploa.* The anther appendages are large and densely glanduliferous with some glands occurring below on the connective. The sclerified ring at the base of the style is narrower than in *Lepidaploa,* and there is a much broader basal attachment inside the ring. Finally, the inflorescence is the type with many primary branches that is common in *Chrysolaena* and that shows a high percentage of heads that are long-pedunculate because they are at the apices of primary branches. The seriately cymose or repeatedly proliferated cymose condition within each primary branch in the two new species is only weakly developed, with no more than three heads in a series. Even the new *C. hatschbachii,* which has the seriate condition most developed, has the branches with distinctive elongate basal internodes and many distal proliferations that revert to the vegetative leafy form. Other species of *Chrysolaena,* such as *C. platensis,* are closer to *Lepidaploa* in their longer seriate cymes.

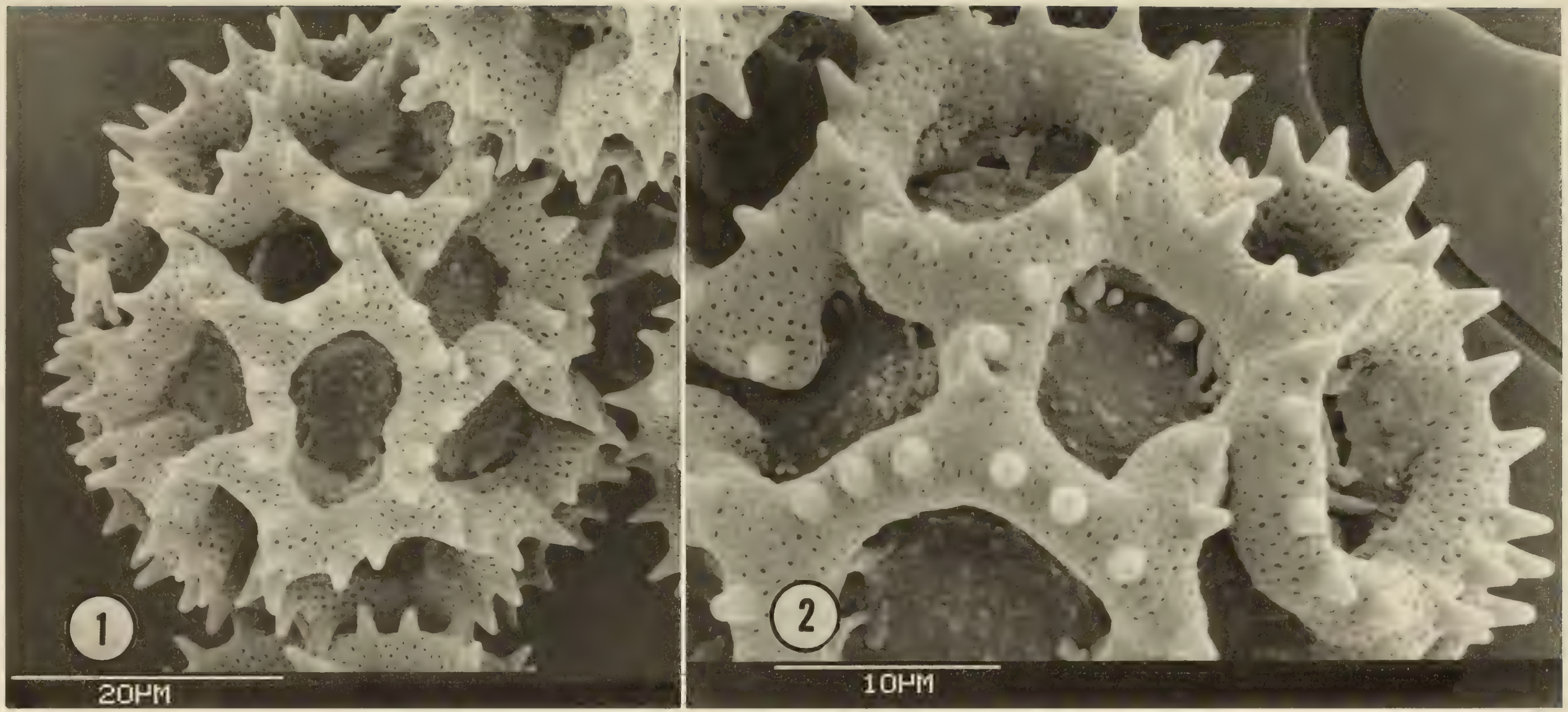
The two new species were originally considered as variants of one species, but differences in habit, pubescence, and numbers of floral parts have led to recognition of each at the species level.

Chrysolaena hatschbachii
H. Robinson, sp. nov.
(Figs. 1–3)

Plantae suffrutescentes erectae ad 70 cm altae intermittentiter subverticillate ramosae; caules teretes albo-tomentosae vel sublanatae. Folia alterna erecto-patentia et imbricata superne leniter minores et non remotiores sessilia oblongo-lanceolate 2–4 cm longa 0.7–1.8 cm lata base rotundata margine integra plana vel vix recurvata apice mediocriter acuta supra dense albo-sericea subtus distincte pallidiores dense breviter lanata et tomentella non glandulifera, nervis secundariis ascendentibus basilaribus leniter validioribus. Inflorescentiae terminales sub capitulis primariis subumbellate proliferentes, ramis 5–6 cm longis plerumque ebracteatis in capitulis secundariis et tertiariis terminatis sub capitulis secundariis et tertiariis plerumque in ramis foliiferis elongatis proliferatis, ramis dense patentiter breviter albo-sublanatis et tomentellis. Capitula ca. 12 mm alta et lata; bracteae involucri ca. 25 leniter inaequales 2–3-seriatae oblongo-lanceolatae 6–7 mm longae ad 2 mm latae apice leniter reflexae extus albo-tomentosae. Flores ca. 15 in capitulo; corollae lilacinae 10–11 mm longae anguste infundibulares plerumque glabrae, tubis ca. 4 mm longis, faucibus ca. 1.3 mm longis, lobis linearibus 4.5–5.0 mm longis ca. 0.7 mm latis apice non vel pauce minute spiculiferis et dense glanduliferis; thecae antherarum ca. 3 mm longae; appendices antherarum anguste ovatae ca. 1 mm longae dense glanduliferae; basi stylorum anguste annulate scleroidei. Achaenia ca. 2.3 mm longa dense setulifera; setae pappi biseriatae, interiores ca. 7 mm longae, squamae exteriores oblongo-ellipticae ca. 1.5 mm longae. Grana pollinis in diametro ca. 55–60 μm echinolophata.

Type.—Brazil: Paraná; Mun. Piraí do Sul: Estrada do Cerne, Serra das Furnas; campo seco, arenoso da borda dos peraus; ereta, 70 cm, capítulos lilás, 19 Nov 1989, *Hatschbach & Nicolack 53574* (holotype MBM; isotype US).

Chrysolaena hatschbachii is most distinctive in its coarse, intermittently subvertillicate branching. Some of the more basal branch clusters seem to be strictly vegetative, but more distal clusters of branches arise from below the heads that terminate the main branches. The new species is most



Figs. 1, 2. *Chrysolaena hatschbachii* pollen; 1, Grain showing perforated tectum restricted to the muri, and the colpus, oriented transversely, extending between the polar areoles; 2, View of the muri showing weak attachment to the foot layer.

closely related to *C. nicolackii,* described below, but the stem and peduncle pubescence is sublanate with a dense tomentellous layer intermixed, the undersurfaces of the leaves have denser and distinctly paler pubescence without evidence of glandular dots, the leaf margins seem less recurved, and the heads seem to have fewer and larger involucral bracts and fewer florets. The species is known thus far from only the type collection from northern Paraná.

Chrysolaena nicolackii
H. Robinson, sp. nov.
(Figs. 4–11)

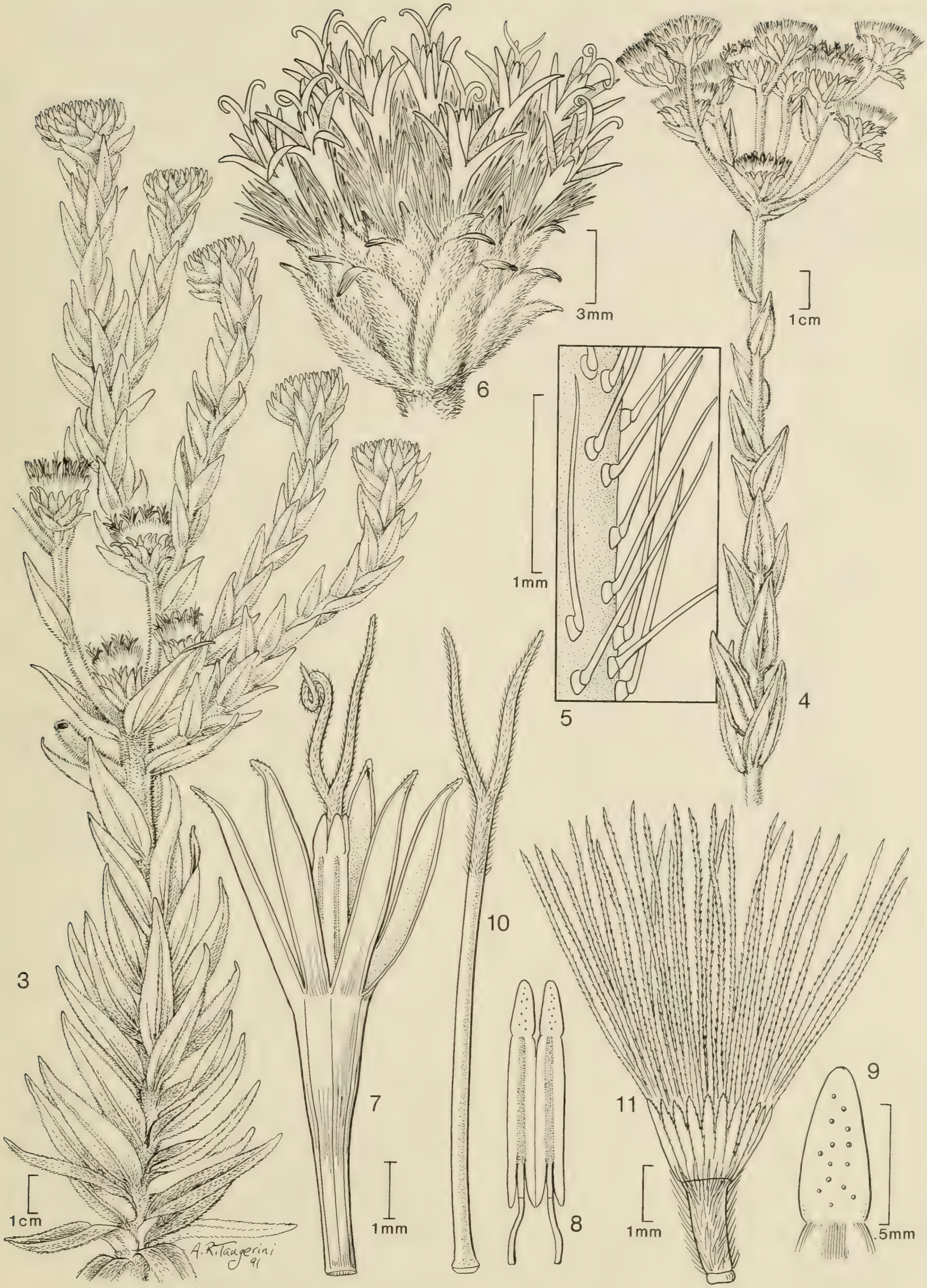
Plantae suffrutescentes plerumque 50–90 cm altae base pauce vel mediocriter ramosae; xylopodium praesens; caules brunnescentes teretes laxe sordide hirsuti superne subsericei. Folia alterna plerumque erecto-patentia et imbricata inferne et superne minoria et remotioria sessilia plerumque oblonga 2.0–5.5 cm longa 0.5–1.8 cm lata base rotundata margine integra anguste recurvata apice breviter acuta supra et subtus laxe sericea subtus vix vel non pallidiora sparse glandulo-punctata, nervis secundariis ascendentibus basilaribus leniter validioribus. Inflorescentiae terminales plerumque subumbellatae, ramis simplicibus et ebracteatis vel seriate bicapitatis et 1–3-bracteatis sordide sericeis et dense tomentellis. Capitula ca. 12 mm alta 13–15 mm lata; bracteae subinvolucri oblongae vel lanceolatae ca. 7 mm longae margine recurvatae, bracteae involucri ca. 35 leniter inaequales 2–3-seriatae oblongo-lanceolatae 4–7 mm longae inferne ad 2 mm latae apice leniter vel distincte reflexae extus dense sordide sericeae. Flores ca. 25–28 in capitulo; corollae lilacinae 10–11 mm longae anguste infundibulares plerumque glabrae, tubis 3.5–4.0 mm longis, faucibus 1.2–1.6 mm longis, lobis linearibus ca. 4.3 mm longis 0.8 mm latis apice breviter pauce spiculiferis et dense glanduliferis; thecae antherarum ca. 3 mm longae; appendices antherarum ovatae ca. 0.8 mm longae dense glanduliferae; basi stylorum anguste annulate scleroidei. Achaenia ca. 2 mm longa dense setulifera, rhaphidibus elongatis; setae pappi biseriatae, interiores 6–7 mm longae superne vix vel non latiores, squamae exteriores oblongo-ellipticae ca. 1.5 mm longae. Grana pollinis in diametro ca. 65 μm echinolophata.

Type.—Brazil: Paraná; Mun. Campo Largo: Serra São Luiz do Purunã; afloramentos de arenito (borda da Cuesta Devoniana); subarbusto 90 cm, capítulos lilás; 12 Jan 1990, Cordeiro & Nicolack 682 (holotype MBM; isotype US). Paratypes: Brazil: Paraná; Rodovia do Café, Rio Tibagi, Ponta Grossa; campo, 900 m; erva, flôr roxa, 12 Dec 1965, Reitz & Klein 17488 (US). Mun. Campo Largo: Rio Papagaios, campo limpo; capítulos lilás, 18 Dec 1960, Hatschbach 7543 (MBM, US).

Chrysolaena nicolackii is closest to *C. hatschbachii* and was initially regarded as the same species. However, the number of differences are considerable. The plants are more sericeous, the pubescence is browner and that of the leaf surfaces is sparser and nearly concolorous, glandular punctations are evident on the abaxial surfaces of the leaves, the leaves toward the bases and tops of the plants are reduced, the margins of the leaves and subinvolucral bracts are narrowly but distinctly recurved, the involucral bracts are more numerous, and there are ca. 25–28 rather than ca. 15 florets. Only one specimen of either of the new species has a base showing a distinct woody tuber, but such a base is presumably characteristic of both species and of the entire genus.

Nine species are presently recognized in *Chrysolaena.* They can be distinguished by the following key that is partially derived from the key to *Vernonia* series *Flexuosae* of Jones (1981).

1. Largest leaves at or near base, rarely with small leaves evident below the largest leaves 2
   2. Leaves almost all basal; inflorescence borne on a long, essentially leafless scape, with abrupt sub-



Figs. 3–11. *Chrysolaena* sp. nov. 3, *C. hatschbachii* H. Robinson, flowering branch showing vegetative proliferations. Figs. 4–11. *C. nicolackii* H. Robinson. 4, Flowering branch; 5, Hairs of upper leaf surface; 6, Head; 7, Corolla with anthers and style; 8, Anthers; 9, Anther appendage showing positions of glands; 10, Style showing narrow sclerified ring at base; 11, Achene.

umbellate branching above, sometimes with a solitary head .... *C. oligophylla*

2. Leaves not all basal, present but strongly reduced above; inflorescence with lax, seriately cymose branches.................... 3

3. Heads with 28–65 florets; corollas glabrous; basal leaves oblanceolate .... *C. flexuosa*

3. Heads with 15–26 florets; corollas often with glands at tips of lobes; basal leaves elliptic-ovate............. *C. propingua*

1. Largest leaves distinctly above base, usually with distinct, smaller leaves below.......................... 4

4. Involucral bracts with slightly but distinctly reflexed tips; style with a narrow ring of sclerified cells at base......................... 5

5. Plants with leafy stems produced from subverticillate clusters of branches, sometimes arising from the branches of the inflorescence; pubescence on the abaxial surface of the leaves distinctly paler than that of the adaxial surface, densely covering the surface; heads with ca. 25 involucral bracts and ca. 15 florets .... *C. hatschbachii*

5. Plants without subverticillate branching, with reduced leaves below inflorescence; pubescence on leaf surfaces nearly concolorous, the abaxial surface partially visable and showing some glandular punctations; heads with ca. 35 involucral bracts and ca. 25–28 florets .... *C. nicolackii*

4. Involucral bracts without reflexed tips; style base without a ring of sclerified cells 6

6. Leaves broadly oblong, ovate or obovate, abaxial surface of the leaves often densely velvety tomentose with golden-brown, flexuous hairs 7

7. Heads with 10–21 florets; involucre 5–10 mm high, with inner involucral bracts 5–8 mm long; anther appendages often without glands .. *C. herbacea*

7. Heads with ca. 30–40 florets; involucre 10–15 mm high, with inner involucral bracts 9–13 mm long; anther appendages with glands .... *C. verbascifolia*

6. Leaves narrow; abaxial surface of the leaves sparsely to densely sericeous with whitish or pale yellowish, stiff hairs 8

8. Heads with 10–27 florets; leaves elliptical, oblanceolate, or linear-elliptical; stems 5–20 dm tall; achenes 1.2–3.0 mm long, strigose .... *C. platensis*

8. Heads with 30–44 florets; leaves linear-lanceolate; stems 2.5–4.2 dm tall; achenes 1.5–1.8 mm long, sparsely hirsute-villous .. .. *C. lithospermifolia*

Acknowledgments

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THREE NEW SPECIES OF *JUSTICIA* (ACANTHACEAE) FROM BRAZIL

Dieter C. Wasshausen

Abstract.—Three new species of *Justicia* (sect. *Chaetothylax*) from Brazil, *J. andersonii, J. harleyi,* and *J. matogrossensis* are described, illustrated, and compared with their closest relatives.

Justicia is the largest and taxonomically the most complex genus of the Acanthaceae, with between 420 (Mabberley 1987) and ca. 600 (Graham 1988) species worldwide. The taxonomic history of the genus is rather complex; recently Graham (1988) attempted an overall schematic delimitation of the taxa in this assemblage of dissimilar elements. By utilizing characters of inflorescence, androecium, pollen, and seeds, she proposed the broadest definition of *Justicia* yet to date. This paper attempts to deal only with the taxa in section *Chaetothylax* (Nees) V. A. W. Graham.

Nees von Esenbeck (1847a) described the genus *Chaetothylax* with a single species, *C. tocantinus,* from Goías, Brazil. Later that same year in A. P. de Candolle's *Prodromus* (1847b) he published two additional species, *C. phyllostachyus* from Mexico (precise section presently not known, but definitely not sect. *Chaetothylax*) and *C. umbrosus* from Colombia and Argentina. Presently, twelve species are recognized by this author as distinctly belonging in this section. These species occur in Guatemala and Nicaragua (*C. rothschuhii* Lindau), Venezuela and Colombia (*C. haughtii* Leonard, *C. huilensis* Leonard, *C. rothschuhii* Lindau), Peru (*J. soukupii* (Standl. & Barkl.) V. A. W. Graham), Bolivia (*C. boliviensis* Lindau), Brazil (*C. eranthemanthus* Rizzini, *C. hatschbachii* Leonard, *C. tocantinus* Nees), as well as the three new taxa, and Paraguay and Argentina (*C. umbrosus* Nees).

The genus *Chaetothylax* was previously characterized by a long tubular corolla with small, short lips and by the lower anther theca being much smaller than the upper, the smaller one usually inserted much lower on the connective, calcarate, often sterile, and sometimes reduced to a short filiform appendage. Graham (1988) distinguished the expanded new sect. *Chaetothylax* by the long, cylindrical corolla tube that clearly exceeds the length of the upper lip. However, this characteristic has also been used to distinguish *Siphonoglossa,* another genus of controversial standing. The latter genus has, in addition, bithecous anthers, with the thecae more or less superposed and equal. Graham (1988) placed *Siphonoglossa* into synonymy in *Justicia* sect. *Chaetothylax.* I provisionally accept this disposition of *Chaetothylax* and *Siphonoglossa* in *Justicia.* Nevertheless, I believe that additional data on inflorescence types, floral characters, and pollen types must be analyzed for a larger number of species throughout their range to identify relatively homogeneous natural groups before one can fully resolve the disposition of these genera.

Key to the Presently Recognized Species of the Genus *Justicia* sect. *Chaetothylax*

1. Spikes relatively narrow, to 5 mm wide 2
1. Spikes 8–20 mm wide 3
2(1). Corollas 12 mm long, the lips lilac, the tube 7 mm long, 1.5–2 mm wide, whitish; bracts su-

bulate, 0.5 mm wide at the base, carinate. Brazil .... *Chaetothylax hatschbachii*

2(1). Corollas 15–17 mm long, violet to white, the tube narrow 11 mm long, 0.6 mm wide; bracts lanceolate, 0.75 m wide. Paraguay, Argentina .... *J. goudotii* (*Chaetothylax umbrosus*)

3(1). Bracts lanceolate, oblanceolate to broadly oblanceolate, 2–6 mm wide 4

3(1). Bracts filiform, linear, linear-subulate or linear-lanceolate, 0.4–1.5 mm wide 5

4(3). Corollas white, 20 mm long, the tube 15 mm long; bracts 11–13 mm long, 5–6 mm wide. Brazil .... *J. andersonii*

4(3). Corollas white tinged with pink, 17 mm long, the tube 11 mm long; bracts 8–9 mm long, 2–3 mm wide. Peru ... *J. soukupii*

5(3). Corollas white. Guatemala, Nicaragua, Venezuela, Colombia, Ecuador .... *Chaetothylax rothschuhii*

5(3). Corollas violet, pink, purple, purplish red, magenta or red .. 6

6(5). Corollas 13–15 mm long 7

6(5). Corollas 20–32 mm long 8

7(6). Herbs to 30 cm tall; bracts 12 × 0.5 mm, ciliate and hirsute; corolla tube subcylindric, 12 mm long, densely hirtellous. Colombia .. *Chaetothylax huilensis*

7(6). Suffrutescent herbs to 1 m tall; bracts 5 × 0.75 mm, minutely pilose; corolla tube narrowly cylindric, 7 mm long, pilose. Bolivia, Brazil, Paraguay .... *Chaetothylax boliviensis*

8(6). Corolla tube obconical elongate, curved inwards, 2 mm wide at the base, narrowed to 1 mm at 3 mm above the base, thence expanded to 4 mm at the throat, the lips 15–18 mm long. Brazil .... *J. tocantina*

8(6). Corolla tube narrowly cylindric, straight, the straight portion 0.75–1 mm wide, enlarged at the base 1–1.5 mm and at the mouth 1.5–3 mm, the lips 4–7 mm long............... 9

9(8). Bracts and bracteoles extremely small, 1–3 mm long. Brazil *Chaetothylax eranthemanthus*

9(8). Bracts and bracteoles 5–8.5 mm long 10

10(9). Corollas 20 mm long, purple; bracts 7.5–8.5 mm long, 1.3–1.5 mm wide, pilose; calyx segments 7 mm long, 0.4 mm wide, conspicuously puberulous. Brazil .... *J. matogrossensis*

10(9). Corollas 25–28 mm long, magenta or pink with paler tube; bracts to 7 mm long, 0.5–1 mm wide, hirtellous or moderately hirsute; calyx segments 8.5–10 mm long, 0.5–0.75 mm wide, moderately to sparingly hirtellous or puberulous 11

11(10). Corolla tube 24 mm long; leaf blades oblong; bracts, bracteoles and calyx segments sparingly to moderately hirtellous, not conspicuously glandular. Colombia .. *Chaetothylax haughtii*

11(10). Corolla tube 14 mm long; leaf blades elliptic to ovate; bracts, bracteoles and calyx segments hirsute and distinctly bearing minute yellowish glands. Brazil .... *J. harleyi*

Many of the new combinations of *Chaetothylax* species to *Justicia* have not yet been made, hence, these species are cited in the key as *Chaetothylax*. Furthermore, the taxon *Chaetothylax leucanthus* Leonard (1958) from Colombia should be placed into synonymy under *Chaetothylax rothschuhii* Lindau (1895).

Justicia (sect. *Chaetothylax*) *andersonii* Wasshausen, sp. nov.

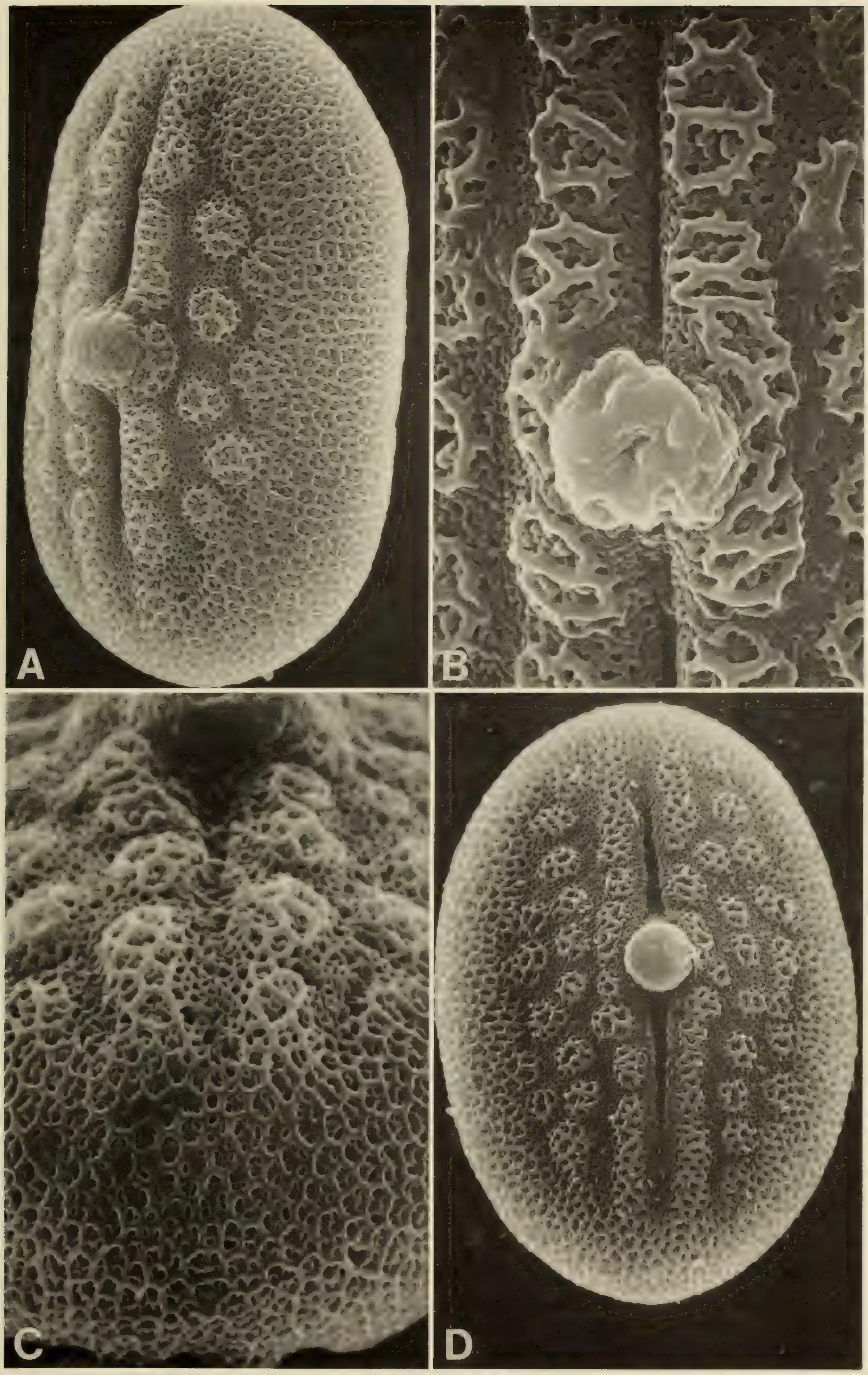
Figs. 1A–C, 2A–D

Herba, caulibus erectis vel ascendentibus, bifariam puberulis; foliorum lamina oblonga-ovata, obtusa vel acuta et aristata, basi cuneata in petiolum decurrens, aliquanto firma, utrinque glabra vel subglabra, costa et venis lateralibus parce hirtella; petioli hirtelli; paniculae axillares et terminales, subsessiles, ex spicis densis floribus; bracteae oblanceolatae, gradatim angustatae et cuspidatae, reticulatae, virides, parce pilosae et glanduloso-punctatae; bracteolae lineares, virides; calycis segmenta 4, albido-viridia, linearia, puberula et minute glanduloso-punctata, ciliata; corolla alba, glabra praeter medium et labio pagina exteriore, tubo cylindrico, labiis subaequalibus, labio superiore anguste ovato, apice rotundato vel obtuso, integro, labio inferiore ovato, trilobato, lobis obovatis, rotundatis vel obtusis, hirtellis; stamina exserta, lobis antherarum superpositis, lobo superiore fertili, lobo inferiore sterili, reducto.

Herbaceous, erect or ascending plants 15–25 cm tall; stems bifariously pubescent with sordid, recurved eglandular trichomes; leaves petiolate, the blades oblong-ovate, 7–10 cm long and 2.7–3.7 cm wide, obtuse to acute and often aristate at the apex, narrowed at the base and briefly decurrent on the petiole, rather firm, drying dark green, both surfaces glabrous except the costa and lateral veins (4 or 5 pairs) sparingly hirtellous, the trichomes sordid and recurved, the cystoliths conspicuous under a lens, especially on the upper surface; petioles slender, 1–2 cm long, sparing hirtellous or the channel densely so, the trichomes scattered, sordid, to 0.35 mm long; flowers borne in axillary and terminal, subsessile panicles to 4 cm long and 2 cm wide, these composed of dense spikes 2.5 cm long and 1–1.5 cm wide and intermixed with small leaves, the lowermost internodes of the spikes 2 mm long, the others successively shorter, hirtellous and glandular, the eglandular trichomes recurved, ascending; bracts oblanceolate, 11–13 mm long, 5–6 mm wide, gradually narrowed and cuspidate, the cusp 1 mm long or more, cuneate at the base, reticulate, green, minutely dotted with yellowish glands, pilose, especially on the veins, the margins ciliate; intermediate bracts linear, 10–11 mm long, 0.5 mm wide, green, sparingly hirsute; bracteoles linear, 9 mm long, 1 mm wide, gradually acuminate, rigid, green, sparingly pilose and minutely gland-dotted, the margins ciliate; calyx whitish-green, 7 mm long, the segments 4, linear, 6 mm long, 0.5 mm wide, puberulous and minutely gland-dotted, the trichomes to 1 mm long, ciliate; corolla white, 2 cm long, glabrous except the medial portion and the outer surface of the lips hirtellous, the trichomes spreading, the tube cylindrical, 1.5 cm long, 2 mm wide at the base, then narrowed to 1.2 mm at 6 mm above the base, 2 mm broad at the mouth, the lips spreading, the upper lip narrowly ovate, about 7 mm long and 1.5 mm wide, entire, emarginate or slightly 2-lobed at the tip, the lower lip ovate, 8 mm long and 7 mm wide, 3-lobed at the apex, the lobes obovate, rounded or obtuse at the apex, hirtellous, the lateral ones 2 mm long and 1.5 mm wide, the middle one about 3 mm long and wide; stamens exserted about 4 mm beyond the mouth of the corolla tube, the upper anther lobe oblong, 1-celled, 1.5 mm long and 0.5 mm thick, the lower lobe sterile and reduced, about 0.75 mm long, calcarate, af-

→

Fig. 1. SEM photomicrographs of *Justicia* sect. *Chaetothylax* pollen. A–C, *Justicia andersonii* (Anderson 9225); D, *Justicia matogrossensis* (Ratter et al. 1911). A, Equatorial view, ×2000. B, Portion of surface, including pore at ×6000, C. Polar orientation, ×3500. D, Equatorial view, ×1800.


A
B
C
D

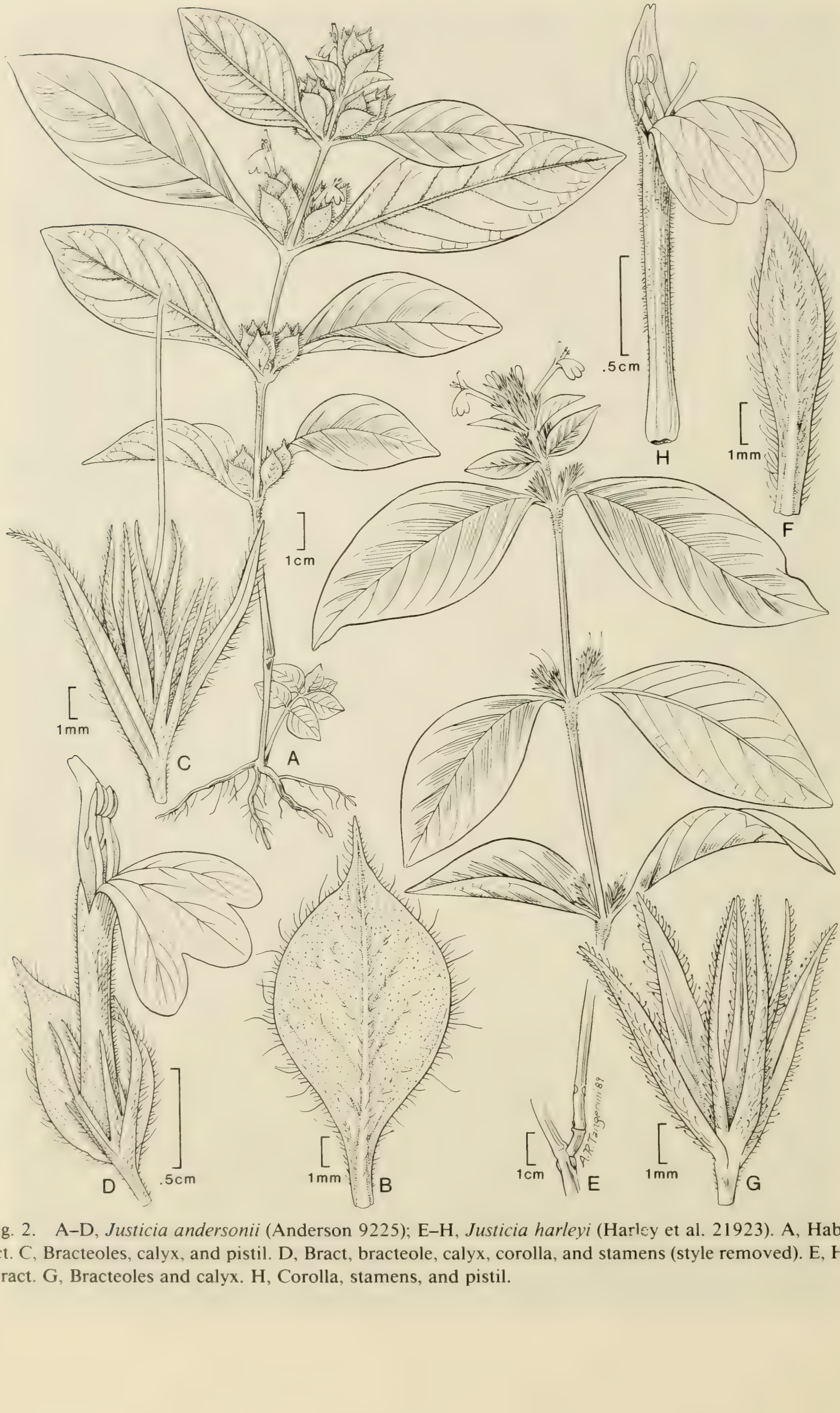


Fig. 2. A–D, *Justicia andersonii* (Anderson 9225); E–H, *Justicia harleyi* (Harley et al. 21923). A, Habit. B, Bract. C, Bracteoles, calyx, and pistil. D, Bract, bracteole, calyx, corolla, and stamens (style removed). E, Habit. F, Bract. G, Bracteoles and calyx. H, Corolla, stamens, and pistil.

fixed about 1 mm below the upper, vestigial; filaments flattened, glabrous; pollen 2-porate, bilateral, prolate, 47 × 27 μm, the trema area micro-reticulate, traversed by 4 rows of 5 or 6 insulae (Fig. 1A–C); style filiform, about as long as the stamens; ovary glabrous; capsule not seen.

Type.—Brazil. Minas Gerais: 15 km by road W of Januária on road to Serra das Araras, 575–650 m alt, 20 Apr 1973, William R. Anderson 9225 (holotype UB; isotypes NY, US).

Distribution.—Hill of coarse, jagged limestone and tall forest at its base, known only from the type locality.

Justicia andersonii is not closely allied to the other South American species in sect. *Chaetothylax.* It is perhaps nearest to the Guatemalan *C. cuspidatus* D. Gibson, but differs markedly in that the latter species has a dark pink to pale purple, pubescent corolla 2.5–3 cm long, sparingly pilose and ciliate calyx segments 7–9 × 1 mm, and lanceolate to ovate-lanceolate, acuminate leaf blades 2–6 × 1–2.5 cm. In contrast, *J. andersonii* has a white, glabrous corolla 2 cm long, puberulous and minutely glandular calyx segments 6 × 0.5 mm, and oblong-ovate, obtuse to acute leaf blades 7–10 × 2.7–3.5 cm. Named in honor of the collector, William R. Anderson, in recognition of his valuable contribution to our knowledge of Brazilian Planalto botany.

Justicia (sect. *Chaetothylax*) *harleyi* Wasshausen, sp. nov.

Figs. 2E–H, 3

Herba gracilis; caulibus subquadrangularibus, sursum bifariam puberulis; foliorum lamina elliptica vel ovata, acuta vel subacuminata, basi cuneata in petiolum decurrens, tenuis, supra viridis ad medium, subtus viridis pallida, utrinque glabra vel subglabra, costa parce hirtella; paniculae axillares et terminales, subsessiles, ex spicis densis floribus; bracteae lineari-lanceolatae, apice mucronulatae, obscure virides, modice hirsutae, costa prominenti; bracteolae lineares, obscure virides; calycis segmenta 4, viridia obscura, anguste linearia, puberula et glanduloso-punctata; ciliata; corolla rosea cum tubo pallido, basi glabro, sursum aliquanto dense hirtella, tubo anguste cylindrico, labio superiore suberecto, anguste ovato, apice minute bilobato, labio inferiore patulo, trilobato, lobis obovatis, obtusis; stamina exserta, lobis antherarum superpositis, ambis lobis fertilibus, luteis.

Slender herb to 50 cm high; stems subquadrangular, glabrous below, upwards bifariously pubescent with sordid, recurved eglandular trichomes; leaves short-petiolate, the blades elliptic to ovate, 6–9.5 cm long, 2.5–3.5 cm wide, acute or subacuminate at the apex, cuneate at the base and decurrent on the petiole, thin, entire, the upper surface mid-green, glabrous or nearly so, except the sparingly hirtellous costa, the lower surface pale-green, glabrous or the costa and lateral veins (6–8 pairs) sparingly hirtellous, the cystoliths numerous on both surfaces, conspicuous under a lens; petioles (unwinged portion) to 0.5 mm long, hirtellous, the trichomes disposed more or less in two lines along the edge of the channel; flowers borne in numerous axillary and terminal, subsessile panicles to 3 cm long and 1.5 cm broad, these composed of dense spikes 1–1.5 cm long (excluding the flowers), and 0.8–1 cm wide, intermixed with small leaves, the lowermost internodes of the spike 1–1.5 mm long, the others successively shorter, hirtellous and minutely glandular, the eglandular trichomes recurved, spreading; bracts linear-lanceolate, 7 mm long, 0.8–1 mm wide, mucronulate at apex, dull green, moderately hirsute, especially on the costa and margins, and bearing minute yellowish glands, the trichomes white, straight, mostly spreading, 0.6–1 mm long, the costa prominent; bracteoles linear, 7.5–8 mm long, 0.5 mm wide, mucronulate at the apex, rigid, dull green, the costa prom-

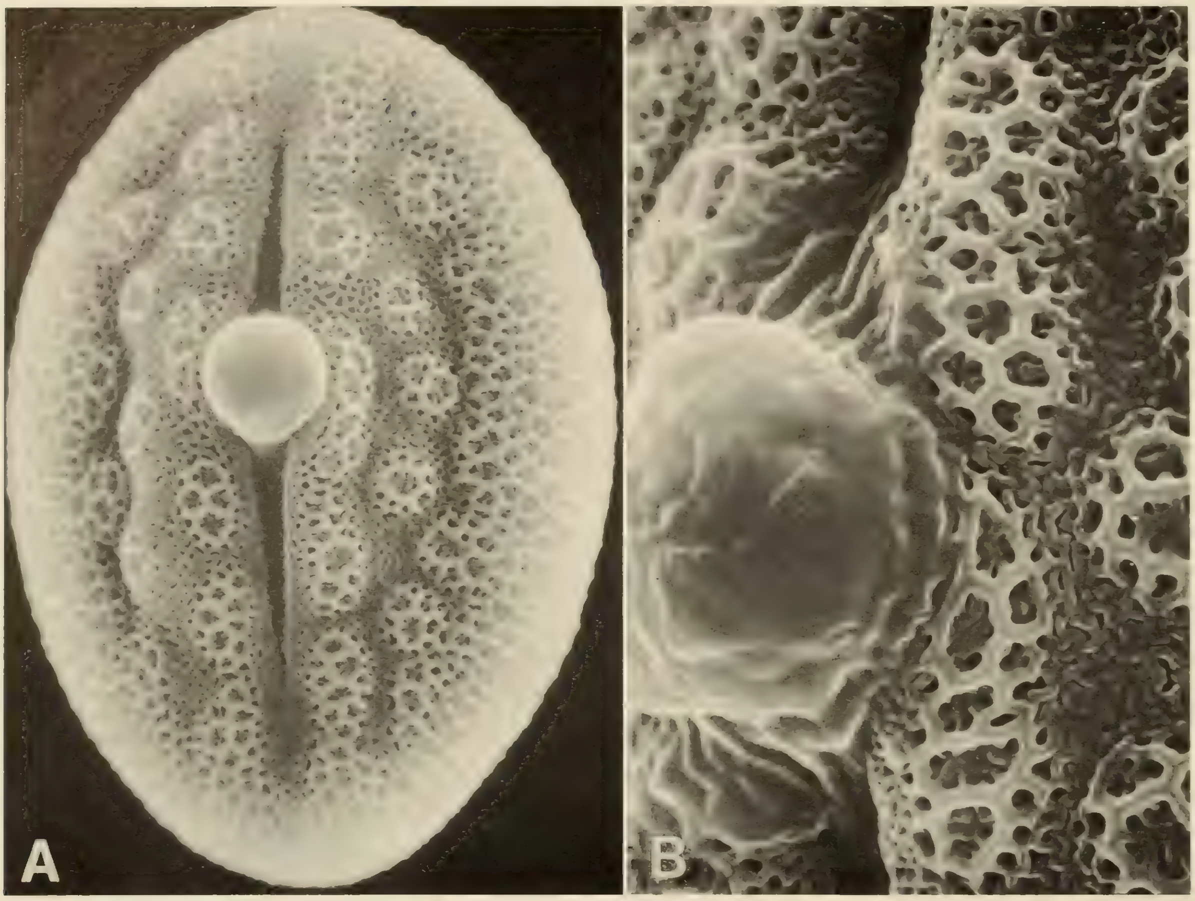


Fig. 3. SEM photomicrographs of *Justicia harleyi* (Harley et al. 21923) pollen. A, Equatorial view, ×2000. B, Portion of surface, including pore at ×5000.

inent, sparingly hirsute, especially on the costa and margins, minutely glandular; calyx dull-green, 9 mm long, the segments 4, narrowly linear, 8.5 mm long, 0.5 mm wide, mucronulate at the apex, the costa prominent, the margins ciliate, glandular puberulous, the trichomes white, mostly straight and spreading, to 0.5 mm long; corolla pink with paler tube, 2.5 cm long, glabrous at base, otherwise rather densely hirtellous with white, straight, spreading or retrorsely curved trichomes, the tube narrowly cylindrical, 1.4 cm long, 1.4 mm wide at the base, 3 mm wide at the mouth, the lips spreading, the upper lip suberect, narrowly ovate, about 5 mm long and 2 mm wide at the base, the tip minutely bilobed, the lower lip with a white patch at the throat, surrounded by darker pink (fide Harley), 7 mm long, 9 mm wide, 3-lobed, the lobes obovate, the middle one 3 mm wide, the lateral ones 2.5 mm wide, all round or obtuse at the apex; stamens exserted about 3.5 mm beyond the mouth of the corolla, glabrous, the upper anther lobe yellow, oblong, 1-celled, 1.1 mm long, 0.4 mm wide, the lower lobe yellow, fertile but reduced, about 0.5 mm long, calcarate, affixed about 1 mm below the upper; filaments white, flattened, glabrous; pollen 2-porate, bilateral, prolate, 47 × 25 μm, the trema area micro-reticulate, traversed by 4 rows of 6 or 7 insulae (Fig. 3); style filiform, just reaching the spur of the lower anther lobe; ovary glabrous; capsule not seen.

Type.—Brazil. Bahia: Chapadão Ocidental da Bahia, 25 km N from Correntina along the Inháumas road, 44°38′W, 13°13′S, alt ca. 600 m, 29 Apr 1980, R. M. Harley, G. L. Bromley, A. M. De Carvalho, J. L. Hage, & H. S. Brito 21923 (holotype CEPLAC; isotypes K, US).

Distribution.—Along roadside through cultivated regions, known only from the type locality.

Justicia harleyi is closely affiliated with *Chaetothylax eranthemanthus* Rizzini, a species from Minas Gerais, Brazil. It is easily separated from *C. eranthemanthus* by its larger bracts, bracteoles, and leaf blades. In *C. eranthemanthus,* the bracts and bracteoles are very small (1–3 mm long), setaceous, and puberulent, the leaf blades are oblong, 4–7 × 1.7–2.7 cm, equally attenuate at both the apex and the base, firm, and crenulate. In contrast, the bracts and bracteoles of the new species are 7 × 0.8–1 mm, mucronulate, hirsute and bearing yellowish glands, the leaf blades are elliptic to ovate, 6–9.5 × 2.5–3.5 cm, acute to subacuminate at the apex, cuneate at the base and decurrent on the petiole, thin, and entire. Named in honor of one of the collectors, Raymond M. Harley, a Labiatae specialist at the Royal Botanic Gardens, Kew.

Justicia (sect. *Chaetothylax*) *matogrossensis* Wasshausen, sp. nov.
Figs. 1, 4A–D

Herba subtilis recta; caulibus subquadrangularibus, sursum bifariam puberulis; foliorum lamina elliptica vel ovata, acuta vel subacuminata, basi cuneata in petiolum decurrens, firma, supra glabra, subtus hirtella, venatione subtus prominenti elevata et flavida; paniculae axillares et terminales, subsessiles, ex spicis densis floribus; bracteae lineari-lanceolatae, apice mucronulatae, virides, pilosae; bracteolae lineares; calycis segmenta 5, 1 segmento redacto, anguste linearia, ciliata et puberula; corolla purpurea, glabra praeter medium et labio pagina exteriore, tubo cylindrico, labiis subaequalibus, labio superiore anguste ovato, integro, obtuso, labio inferiore ovato, trilobato, lobis obovatis, obtusis; stamins vix exserta, lobis antherarum superpositis, lobo superiore fertili, lobo inferiore sterili, reducto, filamentis planis.

Delicate herb to 80 cm high, erect or ascending; stems subquadrangular, glabrous below, upwards bifariously pubescent with sordid, recurved, eglandular trichomes; leaves short-petiolate, the blades elliptic to ovate, 7–9 cm long, 3.5–4.2 cm wide, acute or subacuminate at the apex, attenuate at the base and decurrent on the petiole, rather firm, entire, the upper surface glabrous or nearly so, except the sparingly hirtellous costa, the cystoliths numerous, the lower surface evenly hirtellous, the trichomes erect or slightly curved, spreading or ascending, to 1 mm long, the venation of the lower surface prominent, raised and yellowish (when dry), with 9 or 10 pairs of lateral veins, the venation of the upper surface obscure, the margins ciliolate; petioles (unwinged portion) to 1 cm long, hirtellous; flowers borne in axillary and terminal, subsessile panicles to 2.5 cm long, 1.5–2 cm wide, these composed of dense spikes 1–2 cm long and 0.8–1 cm wide and intermixed with small leaves, the lowermost internodes of the spike 2–4 mm long, others successively shorter, densely hirtellous and minutely glandular, the eglandular trichomes straight, spreading; bracts linear-lanceolate, 7.5–8.5 mm long, 1.3–1.5 mm wide, mucronulate at the apex, green, the costa prominent, pilose, especially on the costa and margins, and bearing minute, yellowish glands, the trichomes white, straight, mostly spreading, 1.25 mm long; bracteoles linear, 7.5–8 mm long, 0.75 mm wide, mucronulate at the apex, rigid, green, the costa prominent, sparingly pilose, especially on the costa and margins, minutely glandular; calyx yellowish-brown, 8.2 mm long, 4 segments narrowly linear, 7 mm long, 0.4 mm wide, mucronulate at the apex, conspicuously puberulous and glandular, the trichomes white, mostly straight and spreading, to 1 mm long, the costa obscure, apparent only toward the base, the margins ciliate, the fifth segment reduced; corolla purple, 2 cm long, glabrous except the hirtellous medial portion and the outer surface of the lips, the trichomes

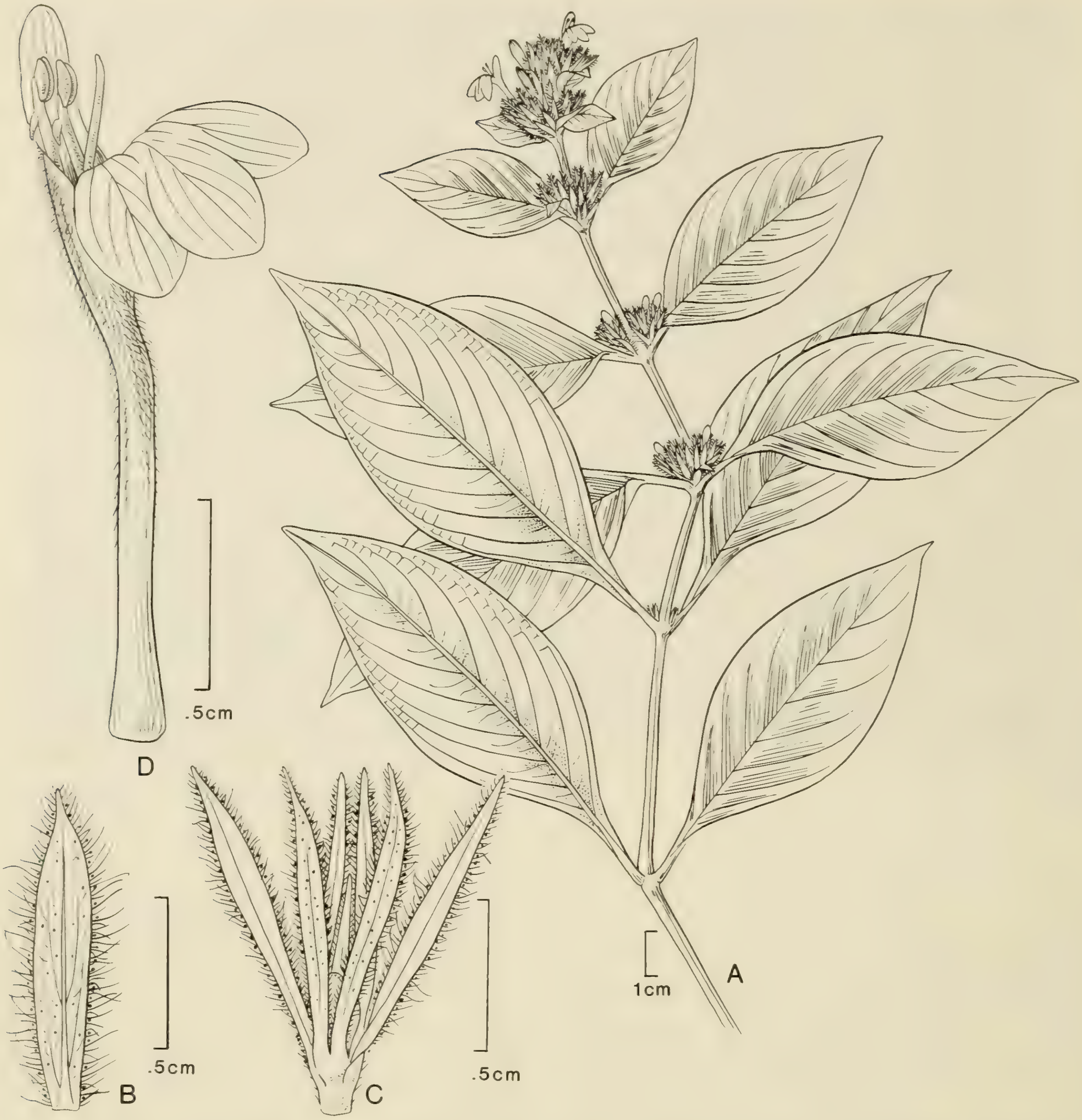


Fig. 4. A–D, *Justicia matogrossensis* (Ratter et al. 1911). A, Habit. B, Bract. C, Bracteoles and calyx. D, Corolla, stamens, and pistil.

spreading, the tube cylindrical, 1.5 cm long, 1 mm wide at the base, then narrowed to 0.75 mm at 9 mm above the base, 2 mm wide at the mouth, the lips spreading, the upper lip narrowly ovate, about 7 mm long, 1.5 mm wide, entire, round or obtuse at the tip, the lower lip ovate, 7 mm long, 7 mm wide, 3-lobed nearly to the base, the lobes obovate, round or obtuse at the apex, hirtellous, the lateral ones 3 mm long, 3 mm wide, the middle one 4 mm long, 3 mm wide; stamens exserted about 4 mm beyond the mouth of the corolla tube, the upper anther lobe oblong, 1-celled, 1 mm long and 0.3 mm thick, the lower lobe sterile and reduced, about 0.8 mm long, calcarate, affixed about 1 mm below the upper, vestigial; filaments flattened, glabrous; pollen 2-porate bilateral, prolate, 40 × 26 μm, the trema area micro-reticulate, traversed by 4 rows of 6 or 7 insulae (Fig. 1D); style filiform, reaching to 0.25 mm below the base of the fertile anther; ovary glabrous; capsule not seen.

Type.—Brazil. Mato Grosso: 8 km E of the Base Camp of Expedition, Base Camp 12°54′S, 51°52′W, ca. 270 km N of Xavantina on the Xavantina-São Felix road, 22 Jun 1968, J. A. Ratter, R. R. de Santos, R. Souza, R. A. de Castro & Andrelinho 1911 (holotype US; isotypes K, NY).

Distribution.—Growing on rich soil on the floor of deciduous valley forest, in the shade of trees and understory bamboo, known only from the type locality.

Justicia matogrossensis is perhaps nearest in relationship to *Chaeothylax rothschuhii,* a widespread species from Guatemala to Ecuador, but differs markedly in that the latter species has linear-subulate bracts 7 × 0.4 mm, these gradually narrowed to a 1 mm long white, aristate tip, ciliate and rather sparingly hirtellous calyx segments, and a white corolla 1.3 cm long that is finely pubescent except at the base. In contrast, *J. matogrossensis* has linear-lanceolate bracts 7.5–8.5 × 1.3–1.5 mm, these mucronulate, conspicuously puberulous and glandular calyx segments, and a purple 2 cm long corolla that is glabrous except for the medial portion and the outer surface of the lips which are hirtellous.

Acknowledgments

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OBSERVATIONS ON AND REDESCRIPTION OF *MEIOMENIA ARENICOLA* SALVINI-PLAWEN, 1985 (MOLLUSCA: APLACOPHORA), AN INTERSTITIAL SOLENOGASTER FROM FORT PIERCE, FLORIDA

M. Patricia Morse and Jon L. Norenburg

Abstract.—The interstitial solenogaster, *Meiomenia arenicola,* is redescribed and illustrated from material collected in coarse sand sediments off Fort Pierce Inlet, Florida. Included are observations of living organisms and comparisons with other interstitial aplacophorans.

Interstitial solenogasters of the subclass Neomeniomorpha occur as part of a molluscan assemblage in coarse sand environments (Swedmark 1968, Scheltema 1978, Morse & Scheltema 1988). The assemblage includes species of the opisthobranch orders Acochlidiacea and Nudibranchia and is known from temperate zones at Crow Neck, Maine (Morse 1976) and San Juan Island, Washington (Morse 1979) and in tropical habitats at Viti Levu, Fiji (Morse 1987) and Belize, Central America (Morse & Norenburg, personal observations). A similar assemblage was found in a subtropical area in coarse to moderately coarse subtidal sediment at several sites off the Fort Pierce Inlet, Florida. Here the solenogasters are represented by at least three species of the subclass Neomeniomorpha and appear to dominate this molluscan assemblage. The species to be discussed here is similar to a species, *Meiomenia arenicola,* tentatively described by Salvini-Plawen (1985) from two specimens (0.6 mm and 1.2 mm) collected from sand at 40 m off the coast of North Carolina (34°45′N, 75°45′W). The following descriptions include observations on living animals and indicate that members of the genus *Meiomenia* Morse, 1979, have morphologies that facilitate movement among sediment particles and characterize these aplacophorans as interstitial.

Materials and Methods

Five sediment samples were collected with a sled dredge during a 10-year period by the R/V *Tursiops,* R/V *Snook,* or R/V *Sunburst* of the Smithsonian Marine Station at Link Port. Two samples were collected in approximately 16 m of water 9.6 Km off the Fort Pierce Inlet (27°29.13′N, 80°11.65′W) and three in 11 m of water at Capron Shoals (27°26.43′N, 80°14.15′W). The sediment, predominantly biogenic carbonates, might be described as moderately coarse shell sand. Sediment was held in buckets from which subsamples were removed and agitated in fresh seawater. Suspended organisms were collected on a 150-μm nylon screen and then resuspended in seawater in petri dishes.

The solenogasters were studied alive (both intact and squashed) or relaxed in 7.5% magnesium chloride in distilled water for subsequent fixation. They were fixed in 70% ethanol or 3% glutaraldehyde in 2 M cacodylate buffer for use in scanning electron microscopy (SEM). For light microscopy, relaxed specimens were placed in Hollande's fluid, embedded in polyester wax, sectioned at 7 μm and stained with Heidenhain's Azan. Four slides of a single serially-sectioned *Meiomenia arenicola* (USNM 86031) and a whole animal fixed in 70% alcohol (USNM 86032) have been deposited in the Division of Mollusks of the National Museum of Natural History, Smithsonian Institution.

Results

Meiomenia arenicola (Fig. 1) are minute aplacophorans measuring up to 1.5 mm in length with an average size of 1.2 mm long and 0.1 mm wide (*n* = 16). About forty additional specimens were of similar size. The body is covered by a coat of scales, spines and spicules (Fig. 18C–G). Characteristic of the genus *Meiomenia* are elongate lateral spicules. Posteriorly the body is slightly flattened with elongate spines distributed around the posterior margin of the body.

The most common spicules are the oval body scales (Fig. 2, BS). These scales are overlapping and attach to the underlying epidermis by a ball-and-socket arrangement, the "socket" located on the anterior half of the scale. Elongate oval paddle scales are scattered in small numbers among the common body scales. These have a projecting basal attachment which anchors the scales into the integument (Fig. 2, PS, BA).

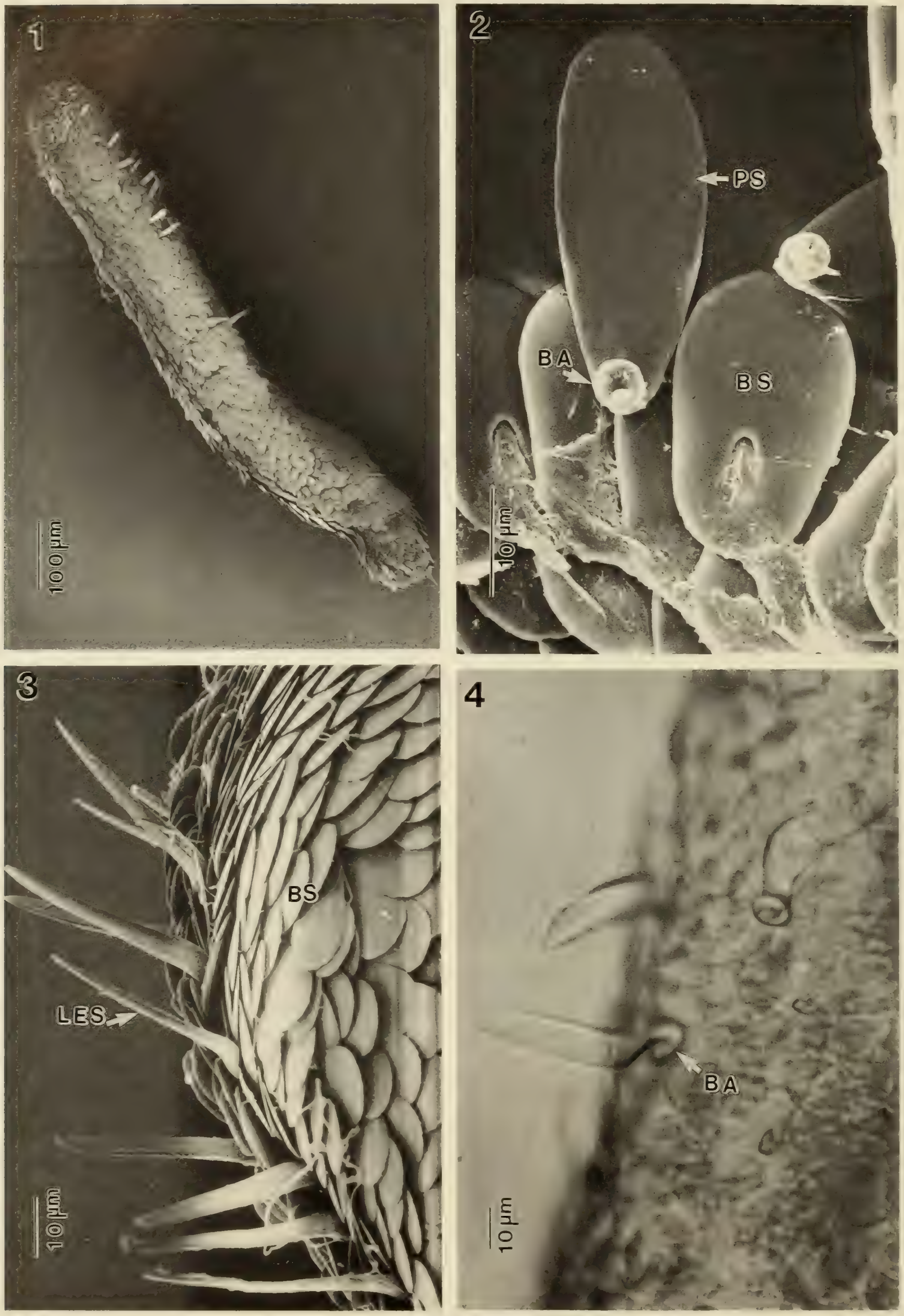
Elongate spines occurring along the lateral surfaces of the body are especially conspicuous on the anterior third of the body. They are slightly flattened and have a characteristic proximal bend and a circular basal attachment (Figs. 3, 4). These lateral spines vary considerably in number, independent of body size, from 5 to 30 or more along the anterior third of the body, and from 0 to 30 or more along the posterior two-thirds of the body. Most commonly there are about 30 in each region. In contrast with the lateral spines of the anterior third, the more posterior spines taper to a point (Fig. 9), and like the anterior spines, are flattened and have a circular basal attachment (Figs. 10, 11). There are usually 5–10 of these pointy spines fringing the caudal margin.

At the anterior end of the crawling animal two protuberances project forward (Fig. 5) as well as bundles of elongate cilia forming three anteriorly projecting bristles. The protuberances can be withdrawn into the vestibule (Fig. 1). Associated with the protuberances are vestibular scales (Figs. 6–8). These minute triangular scales are thickened along their proximal edges and have elaborate basal attachments into the integument. The distal surface is serrated, with some variation in appearance (Figs. 7, 8). The variation may be a result of wear as the smaller scales (Fig. 8) have more elongate serrations. These scales are associated with surfaces that are usually everted as the animal crawls on a slide. Thus the distal margins of these scales would be in constant contact with surrounding sediments.

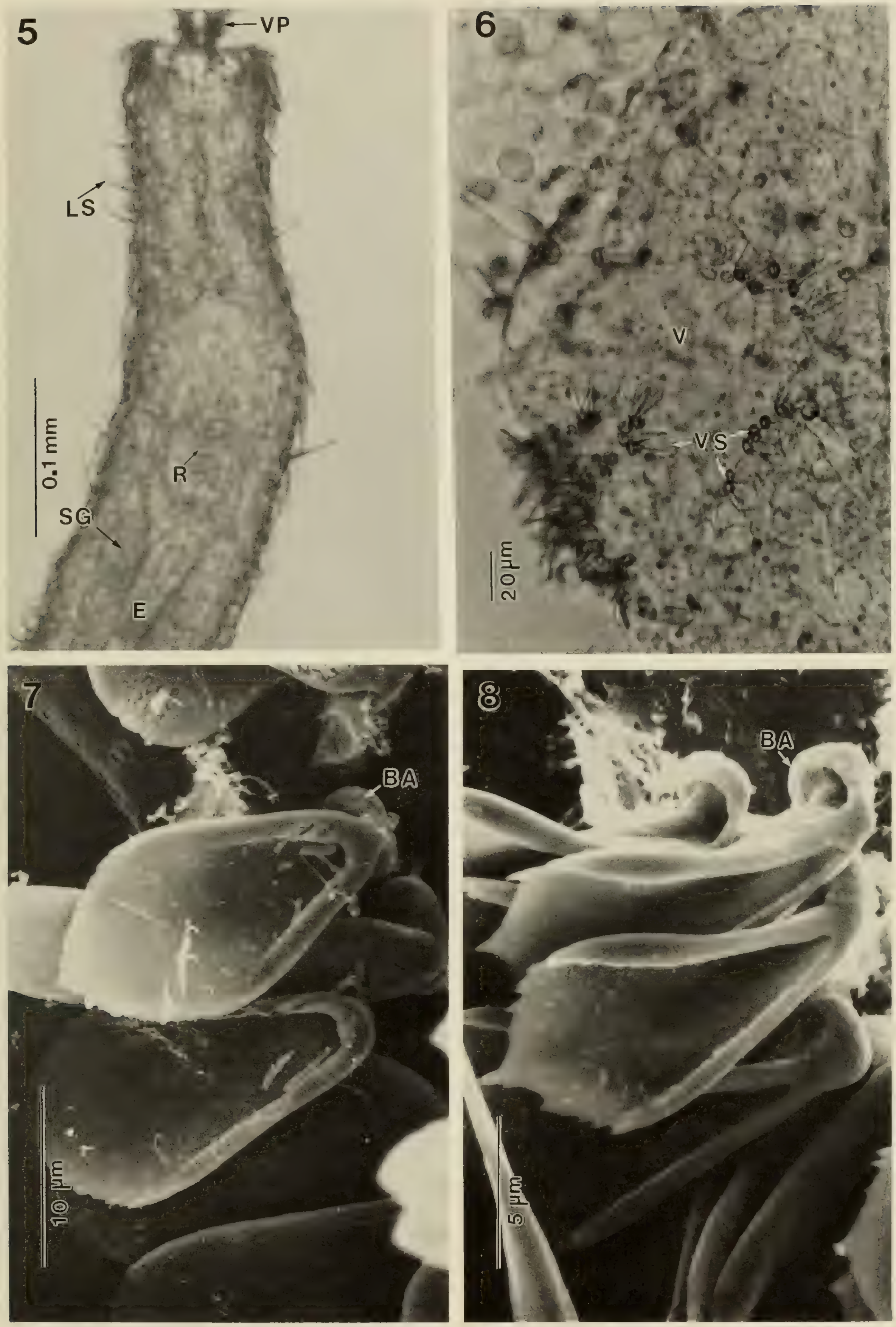
A dorsoterminal organ (dorsoterminal sense organ auctt.), located close to the posterior margin of the body, is surrounded by a variable number (7–10) of small spicules (Figs. 9, 10, 12). On contraction, the organ is directed posteriorly so that it may not be observable. The spicules are approximately triangular, with a point directed medially and often upward, resulting in a crown-like appearance when seen laterally (Fig. 12).

The pedal groove (Fig. 14), which contains the ciliated foot, is along the ventral side, beginning just behind the oral vestibule. The pedal groove is lined on both sides by projecting and overlapping pedal scales (Fig. 13) attached by a ball-and-socket arrangement like that of the body scales. The pedal scales are flattened and elongate with a slight rounding and thickening at the "socket," the point of attachment to the pedal furrow.

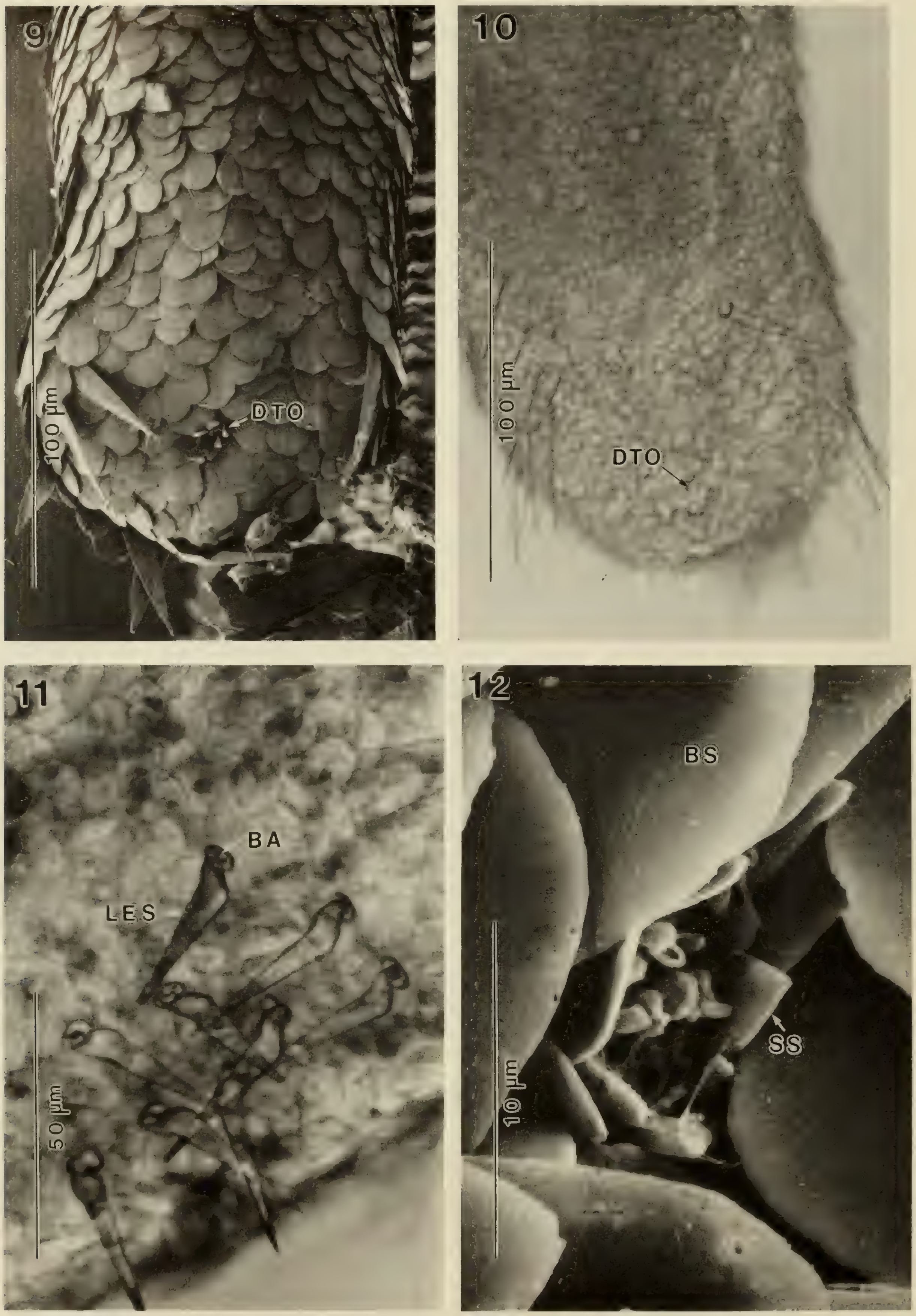
The digestive system (Fig. 5) begins at the mouth opening where a long oral tube leads into the buccal mass that contains the radula (Fig. 5). The radula (Fig. 18A, B) is distichous and consists of eight to twelve (more often 11 or 12) rows of teeth but these are difficult to count with certainty. Each tooth has four denticles. Paired salivary glands (Fig. 5, SG) empty into the buccal cavity, from which the esophagus (Fig. 5) leads pos-



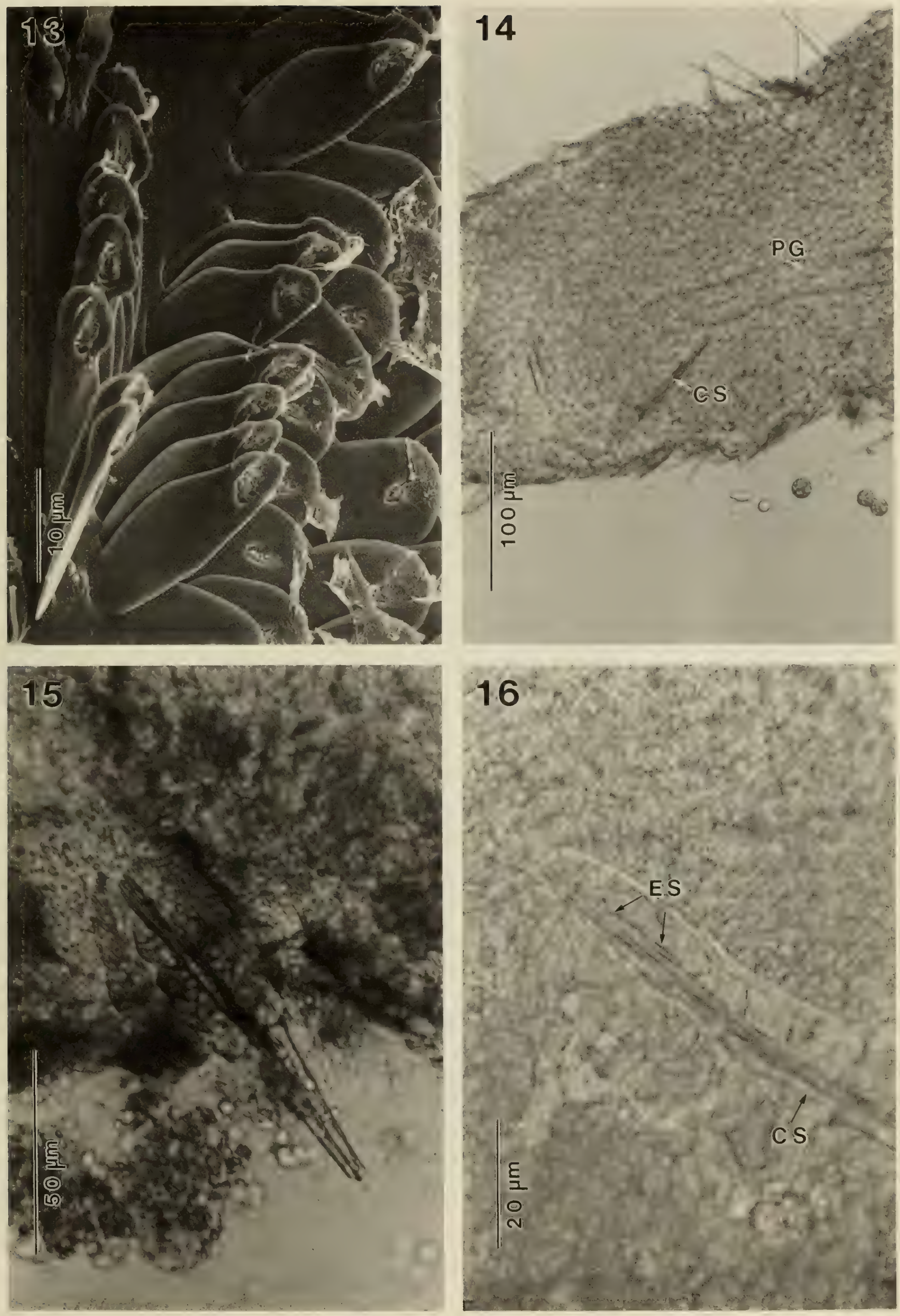
Figs. 1–4. *Meiomenia arenicola* 1, SEM of whole animal; 2, SEM of body spicules showing common oval body scale (BS) with depression for attachment and paddle scale (PS) with round basal attachment (BA); 3, SEM of part of anterior one-third of body showing lateral spines (LES) and overlapping oval body scales (BS); 4, lateral body spines showing the curve and round basal attachment (BA) that is embedded in the body wall.



Figs. 5–8. *Meiomenia arenicola* 5, Anterior end of crawling specimen with everted vestibular protuberances (VP), lateral spines (LS), radula (R), salivary glands (SG) and esophagus (E); 6, Squash preparation of protuberances withdrawn into vestibule (V) showing vestibular scales (VS); 7, SEM of vestibular scales with rounded to triangular distal edge and basal attachment (BA); 8, SEM of vestibular scales with distinct serrations, note central serration and the robust rounded basal attachment (BA) that anchors the scale into the cuticle.



Figs. 9–12. *Meiomenia arenicola* 9, SEM of posterior end showing dorsoterminal organ (DTO) and partial fringe of elongate spines; 10, Posterior end of live specimen with dorsoterminal organ (DTO); 11, Enlargement of posterior lateral elongate spines (LES) showing proximal basal attachment (BA) to the cuticle; 12, SEM of dorsoterminal organ with small scales (SS), surrounded by body scales (BS).



Figs. 13–16. *Meiomenia arenicola* 13, SEM of foot spicules; 14, Posterior end with copulatory spicules (CS) and pedal groove (PG); 15, Squash preparation of copulatory spicule; 16, Prostatic glands and elongate structures (ES) associated with copulatory spicule (CS).

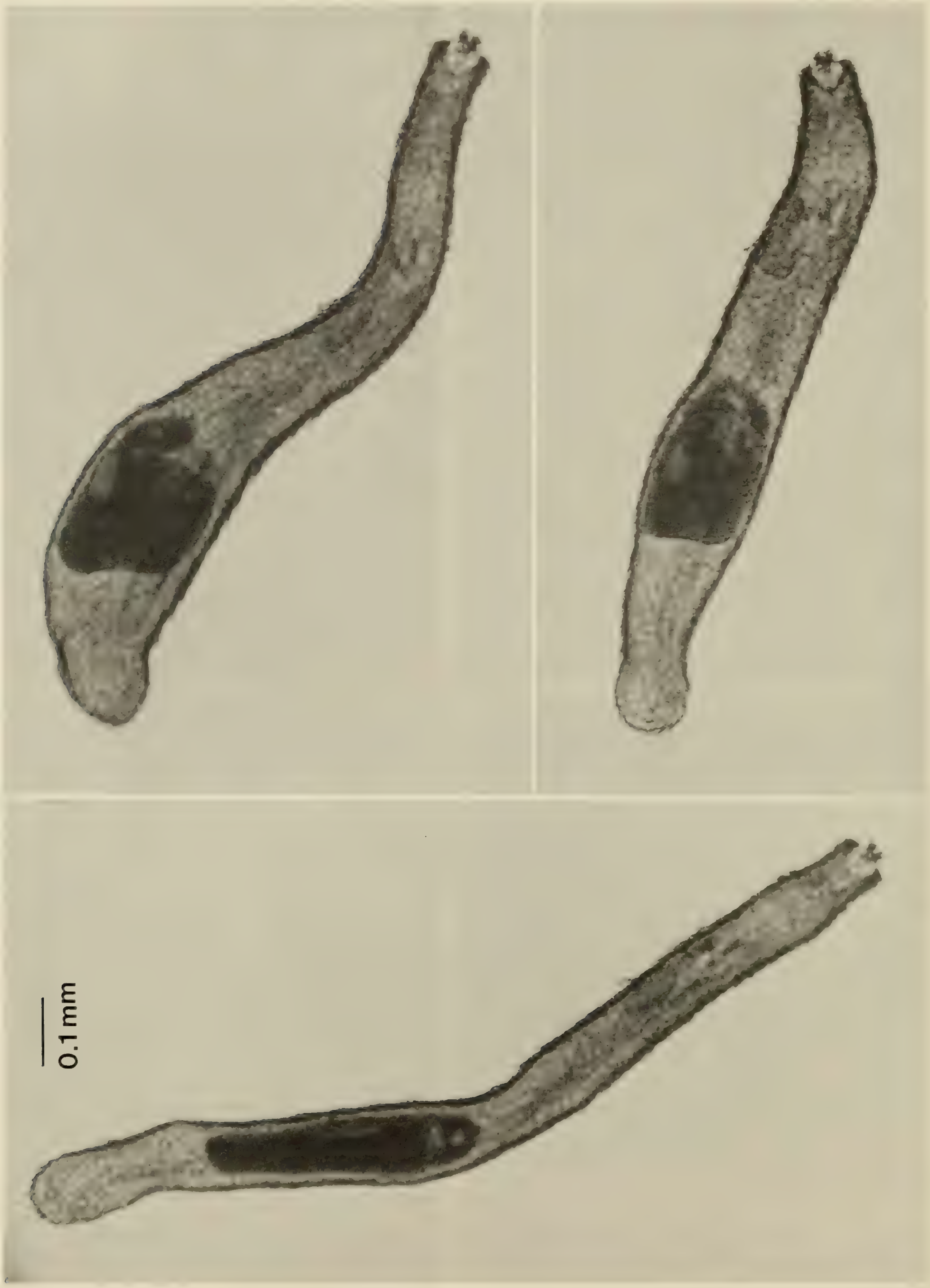


Fig. 17. Three photographs of the same crawling specimen of *Meiomenia arenicola* demonstrating plasticity of body shape and length. Note the dark, posterior vitellogenic eggs.

teriorly into a tubular stomach-intestine, that terminates in the mantle cavity at the end of the pedal groove.

Meiomenia arenicola has been collected in various states of sexual maturity. Copulatory spicules often are noted (Figs. 14–16). Testes are paired elongate sacs lying anterior to the copulatory spicules, and prostatic glands (Fig. 16) are found with the spicules. Copulatory spicules appear to be associated with the presence of recognizable testes as they have not been observed in specimens without recognizable gametes, and a specimen with immature ova had no copulatory spicules. Immature ova have been observed anterior to the copulatory spicules and, in one specimen, a large presumably mature ovum was positioned medially immediately posterior to the copulatory spicules. Large vitellogenic eggs (Fig. 17) often are seen. Packages of minute tubes that might represent packets of sperm were observed associated with the spicules (Fig. 16) but this needs to be verified by further ultrastructural examination.

Meiomenia arenicola is an active aplacophoran that continuously changes its shape while being observed in a glass dish (Fig. 17). The animals move by ciliary gliding or in an inch-worm fashion, contracting and elongating their body, while routinely changing direction and probing with the anterior protuberances as they move. Living animals exhibit a distinct, albeit somewhat weak, adhesive response at the posterior end when disturbed, but a terminal adhesive gland has not been identified.

Discussion

The initial description of *Meiomenia arenicola* by Salvini-Plawen (1985) tentatively placed it in the genus *Meiomenia.* In that paper, the author rediagnosed the genus and noted "without dorsoterminal sense organ." Neither presence nor absence of this organ was part of the original generic diagnosis (Morse 1979) nor is there currently evidence that the dorsoterminal organ found in *M. arenicola* is a sense organ. More studies are needed to determine the functional cytomorphology of the dorsoterminal organs in neomenioids and their relationship to sense organs of other aplacophorans as described by Haszprunar (1987). Usually this organ can be observed only at the relatively high magnification of the compound light microscope or scanning electron microscope, and it was only definitively identified in slightly less than half the specimens

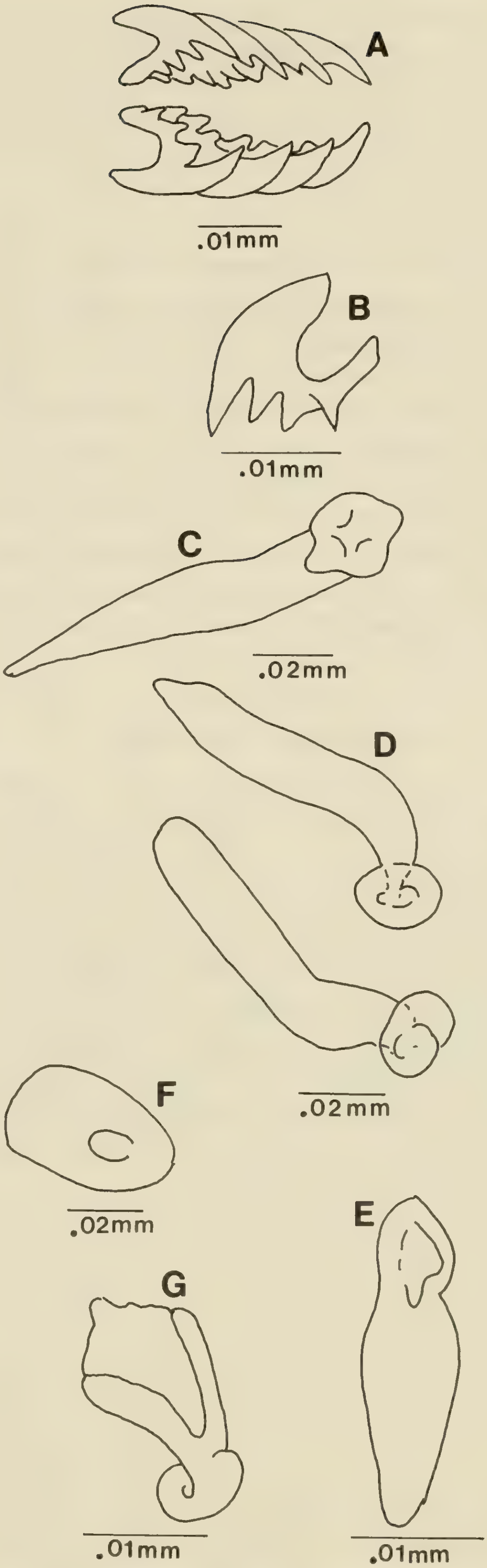


Fig. 18. Diagrams of spicules, spines and radula of *Meiomenia arenicola* A, Group of radular teeth of distichous radula; B, Single radular tooth with four denticles; C, Posterior elongate spine; D, Lateral body spines; E, Pedal spicule; F, Oval body scale; G, Vestibular scale.

so examined. We consider reports of its absence a dubious diagnostic character in the absence of adequate numbers of specimens and therefore by the original genus designation (Morse 1979) this species can be placed in the genus *Meiomenia.*

Meiomenia arenicola can easily be distinguished from *M. swedmarki* Morse, 1979 by the radula. The distichous radula in *M. arenicola* has up to 12 rows and each tooth has four denticles, whereas *M. swedmarki* has 26 rows and each tooth has six denticles. Both of these organisms have elongate body scales with an elaborate basal attachment that may aid in movement through the sediment pore spaces. A single nematocyst was found in a squash preparation of *M. arenicola,* which would suggest that they feed on cnidarians.

Acknowledgments

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A TALE OF TWO SPECIES: TAIL MORPHOLOGY IN PARALARVAL *CHIROTEUTHIS* (CEPHALOPODA: CHIROTEUTHIDAE)

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Abstract.—"Doratopsis" paralarvae of *Chiroteuthis* were observed in-situ and collected intact using a remotely operated vehicle (ROV) in the eastern North Pacific and a manned submersible in the western North Atlantic. These specimens, the first with complete tails, show remarkable interspecific differences in tail morphology but little intraspecific variability. Eleven Pacific specimens had very long rigid tails characterized by pairs of large, fluid-inflated, lateral pouches separated by 4–6 flat, rounded, lateral lobes of tissue (referred to here as flaps, not finlets). The single Atlantic specimen had a long, rigid tail with long, pointed flaps staggered along its sides, each separated by 4–6 short, pointed flaps; when alive, it had what appeared to be very small pouches at the tips of the long flaps. We attribute the Pacific specimens to *Chiroteuthis calyx* Young. Of the species known from the western North Atlantic and Gulf of Mexico, the Atlantic specimen probably is not *C. veranyi* Ferrusac, *C. lacertosa* Verrill, nor *C. joubini* Voss. It most likely is *C. capensis* Voss or an undescribed species.

Squids of the genus *Chiroteuthis* are among the strangest of cephalopods. Adult *Chiroteuthis* look like caricatures of squids. All members of the genus develop through an unusual elongate paralarval stage, designated as the genus *Doratopsis* by Rochebrune (1884) based on *Loligopsis vermicularis* Rüppell, 1845. Ficalbi (1899) demonstrated that "Doratopsis vermicularis" was actually a young stage of *Chiroteuthis veranyi* (Ferrusac, 1835). Although Pfeffer (1900) and Hoyle (1909) disputed this conclusion, Naef (1923) further defended Ficalbi's position and it has been generally accepted since. Recently, Young (1991) redefined the family Chiroteuthidae, giving the primary familial character as development through a doratopsis-type paralarval stage; he provided a detailed unifying diagnosis for the doratopsis stage.

Doratopsis paralarvae have long been known to have a fragile tail that extends posterior to the fins. However, in all specimens reported in the literature to date, the tails have been either broken or missing. Of the published descriptions of doratopsis paralarvae, only one of Ficalbi's (1899, figs. 1–2) and two of Pfeffer's specimens (1912, plate 46, figs. 1–3) had what until now appeared to be substantial portions of the tail intact. Many other descriptions of doratopsis specimens have been published (e.g., Hoyle 1886, Chun 1910, Issel 1927, Berry 1963); the specimens always lack all but a minute stub of the tail. Young (1991) was forced to omit characters of the paralarval tail in his study because the tails are "invariably broken off."

In the course of studies using submersibles, we have videotaped and collected doratopses with their tails intact. We describe here the details of tail morphology and in-situ behavior of the squids. We include descriptions of the doratopses' general morphology for future taxonomic comparisons. We also discuss the identities of the doratopses and speculate on functions of the tail.

Materials and Methods

Pacific specimens.—These unusual squids were first observed and videotaped in-situ during an ongoing series of remotely operated vehicle (ROV) dives in Monterey Canyon by the Monterey Bay Aquarium Research Institute (MBARI). The ROV operators were then challenged to collect one or more specimens whenever possible in future dives. This effort achieved success when three specimens were collected on separate dives. The "detritus sampler" collecting gear consisted of a large-bore, acrylic tube mounted vertically with remotely actuated, rotating covers to seal both ends. The ROV was maneuvered above the squid and then brought slowly downward until the squid was inside the sampler, which was then closed. These specimens were observed alive by one of us (BHR) aboard ship and one was videotaped through a microscope while alive. All three were then sent to the National Museum of Natural History for detailed morphological observations. Additional specimens have been videotaped and collected and attempts have been made to keep them alive for display at the Monterey Bay Aquarium.

Atlantic specimen.—A single specimen was collected along with several other cephalopods by Marsh Youngbluth of the Harbor Branch Oceanographic Institute using the *Johnson Sea-Link* (JSL) manned submersible for a series of nocturnal dives in Bahamian waters. The doratopsis was collected in a detritus sampler similar to that described above. Its tail broke off when it was transferred from the sampler. The live squid and its tail were photographed in an aquarium aboard ship. The specimen and photographic slides were sent to one of us (CFER) at the National Museum of Natural History (NMNH), but material for comparisons was lacking until now. The slides were the source of the details of tail morphology and chromatophore patterns for the live specimen.

All specimens were examined and measured using a dissecting microscope with ocular micrometer. Mantle length (ML) was measured along the dorsal midline from the anterior edge of the mantle to the posterior insertion of the fins (i.e., including the fins beyond the posterior tip of the mantle sensu strictu, which in a doratopsis terminates near the anterior edge of the fins) but excluding the tail.

Observations

Pacific specimens.—Material examined: 1 specimen collected but not videotaped, 44 mm ML, depth 278 m, 6 Aug 1990, 1330–1400 h Pacific Standard Time (PST), 36°42′N, 122°02′W, USNM 817760; 1 specimen videotaped and collected, 49 mm ML, depth 431 m, 7 Nov 1990, 1406 h PST, 36°42′N, 122°02′W, USNM 817761; 1 specimen videotaped and collected, 60 mm ML, depth 302 m, 24–25 Jul 1991, "nighttime," 36°42′N, 122°02′W, USNM 884234.

Other observations: 3 squids videotaped but not collected, (#1) depth 366 m, 5 Oct 1989, "daytime," 36°42′N, 122°02′W; (#2) depth 335 m, 27 Nov 1989, "daytime," 36°42′N, 122°02′W; (#3) depth 384 m, 20 Dec 1989, "daytime," 36°43′N, 121°59′W. 5 other specimens 50–55 mm ML were videotaped and collected. The specimens were examined at MBARI and the videotapes reviewed in detail but because of labelling problems resulting from attempts to maintain the squids alive, the specimens could not be associated with specific videotape sequences and dive data. Data for videotape sequences (all daytime) are as follows: (#4) depth 399 m, 17 June 1991, 36°42′N, 122°02′W; (#5) depth 416 m, 12 Jul 1991, 36°45′N, 122°02′W; (#6) depth 457 m, 6 June 1991, same area but position not recorded; (#7) depth 471 m, 9 Sep 1991, same area but position not recorded; (#8) depth 278 m, 6 Sep 1990, 36°42′N 122°02′W.

Description of animal (Fig. 1A): Tentacles thin but muscular, very long, much longer than ventral arms, with suckers along distal half; tips slightly expanded as clubs with single dorsal keel on all specimens, narrow trabecular membranes present along both sides of sucker-bearing distal half; suckers tetraserial on clubs and stalks. On 44-mm ML specimen single thickened aboral pad at base of each tentacle and series of pad rudiments on aboral side along proximal half of tentacle stalks; on 49-mm and 60-mm ML specimens series of aboral pads well developed along proximal half of stalks. Arms IV≫III>II>I; teeth not apparent on sucker rings of 44-mm ML specimen; on 49-mm and 60-mm ML specimens arm sucker rings with many long sharply pointed teeth across distal half, increasing gradually in length from sides to center. Tentacle sheaths well developed on ventral arms, of vesiculate tissue. Arm-crown pillar gelatinous and vesiculate, short, approximately equal to head length; esophagus centrally located. Head short. Olfactory papillae well developed, finger-like, ventrally located, anterior to statocysts. Eyes of 44-mm ML specimen egg-shaped in lateral view; small end of each oriented anteroventrally, covered with reflective tissue and large ventral chromatophore; eyes on larger specimens round, each covered laterally with reflective tissue, with single, large ventral photophore. Neck very long (ca. ½ ML) and broad (equal to maximum mantle width), longer than head and arm-crown pillar together; gelatinous, strongly and coarsely vesiculate, forming chambers. Digestive gland and gills located near base of funnel at anterior end of mantle cavity; digestive gland bean-shaped, bright red with lateral veneer of reflective tissue in live animal. Ink sac embedded on ventral surface of digestive gland; reflective, with 2 small photophore rudiments on ventral surface; paired photophores on ink sac well developed in 60-mm ML specimen. Mantle terminates posteriorly near anterior insertion of fins; tissue finely vesiculate posteriorly; very delicate integumentary tissue continues posteriorly from mantle tip, covering gladius ventral to fins. Fins broad, width nearly equals length, round except at anterior and posterior insertions where concavities are partly filled with delicate tissue. Chromatophores orange-brown in live specimen, form pronounced stripe along dorsal midline of mantle and neck, along ventral midline of mantle, scattered around ventral edges and entire dorsal surface of fins, on aboral surface of all arms; 2 rows of very small chromatophores aborally along each tentacle; chromatophore patches on tentacle clubs aborally, ventral and dorsal surfaces of head, laterally at posterior end of mantle and near gills/digestive gland; band of small chromatophores around edge of anterior mantle opening; other chromatophores scattered dorsolaterally on mantle, ventrolaterally on funnel and collar. Chromatophores more numerous on 49-mm ML specimen than on 44-mm ML but patterns very similar; chromatophores on 60-mm ML specimen similar to those of 49-mm ML specimen.

Tail morphology (Fig. 2A): Tail very long, longer than total length of specimen from posterior border of fins to arm tips, constricted near posterior border of fins, gradually broadens to midpoint then tapers to accute posterior tip. In live specimens, 5–6 pairs of knob- or ball-like pouches filled with clear fluid spaced along the lateral edges of the tail. Squeezing one pouch appears to cause fluid to flow into adjacent pouches. Pouches slowly deflate when tail breaks so that in preserved specimens they appear to be tightly rolled flaps of skin. Between pouches, lateral edges of tail form series of obtuse flaps that also roll up in preserved specimens; in live animals these flaps appear as serrations between the ball-like pouches. Tissue of tail vesiculate, especially near central gladius. Gladius box-shaped in cross section, with narrow open gap in ven-

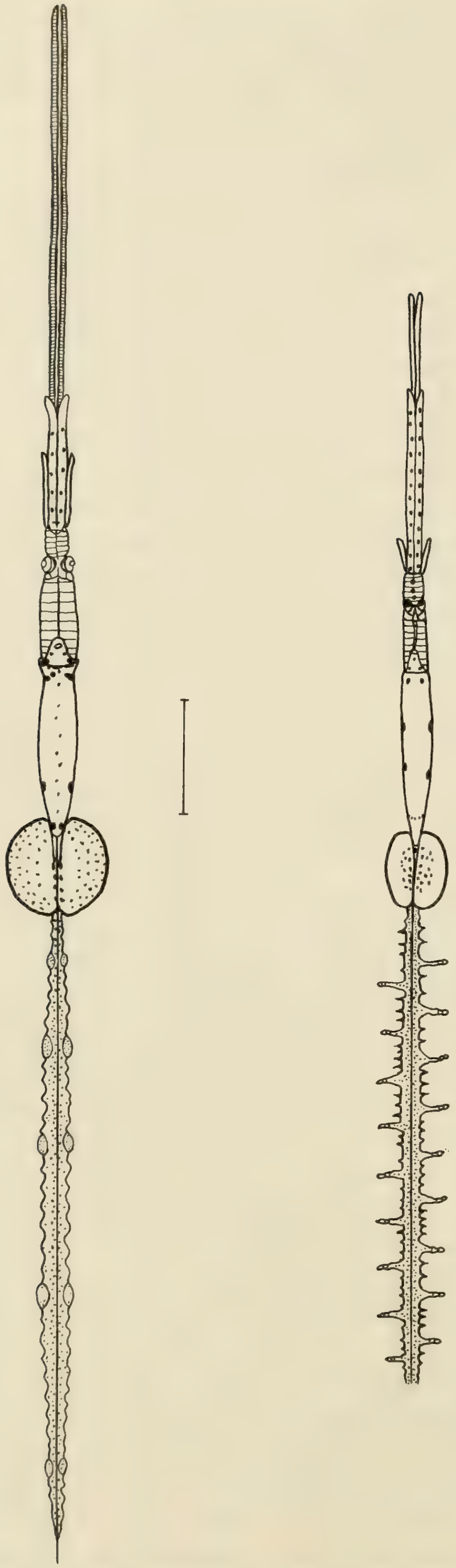

Fig. 1. *Chiroteuthis* spp. Ventral views of doratopsis paralarvae of similar mantle lengths drawn to the same scale. (A, left) Pacific specimen, 44 mm ML, USNM 817760; (B, right) Atlantic specimen, 43 mm ML, USNM 817762. Scale bar = 20 mm.

tral wall and hollow dorsal-midline ridge. Chromatophores concentrated in soft tissue along both sides of gladius, on flaps, and especially on pouches.

Behavior: A typical posture was observed whenever the ROV first approached a doratopsis (Fig. 3). The squids usually orient obliquely, nearly vertically, with the tail pointed downward, the mantle, neck, head, arm-crown pillar, arms, and tentacles approximately in line with the tail. The tentacles extend upward well beyond the tentacle sheaths on the long fourth pair of arms. The arms and tentacles sometimes are spread. The fins undulate slowly. One doratopsis was horizontal in the water when first approached. Another was oriented vertically, head up, but with the arms and tentacles bent 90° at the head so that they hung straight down along the neck and mantle. One individual was observed to bend its gladius more than 45° at the posterior end of the mantle (anterior to the fins) without apparent damage and without breaking the tail.

The doratopsis' escape reaction consists of pointing the tail straight down, then jetting rapidly downward. During the escape, black ink is released in long thin pseudomorphs that undulate slightly in the exhalent current. The pseudomorphs approximate the dimensions and shape of the doratopsis including tail. When attempts were made to collect specimens during videotaping, if they were lightly touched by the side of the sampler, the tail would break completely off close to the narrow constriction near the fins, resulting in the tailless condition always found in net-collected specimens. The breaks always occurred near the fins but not always in exactly the same location, indicating that the break is not associated with a specific weak point in the gladius.

The chromatophores were used by the live animal to form several patterns that, although less complex than those observed in neritic cephalopods, demonstrated the potential for a variety of behavioral patterns

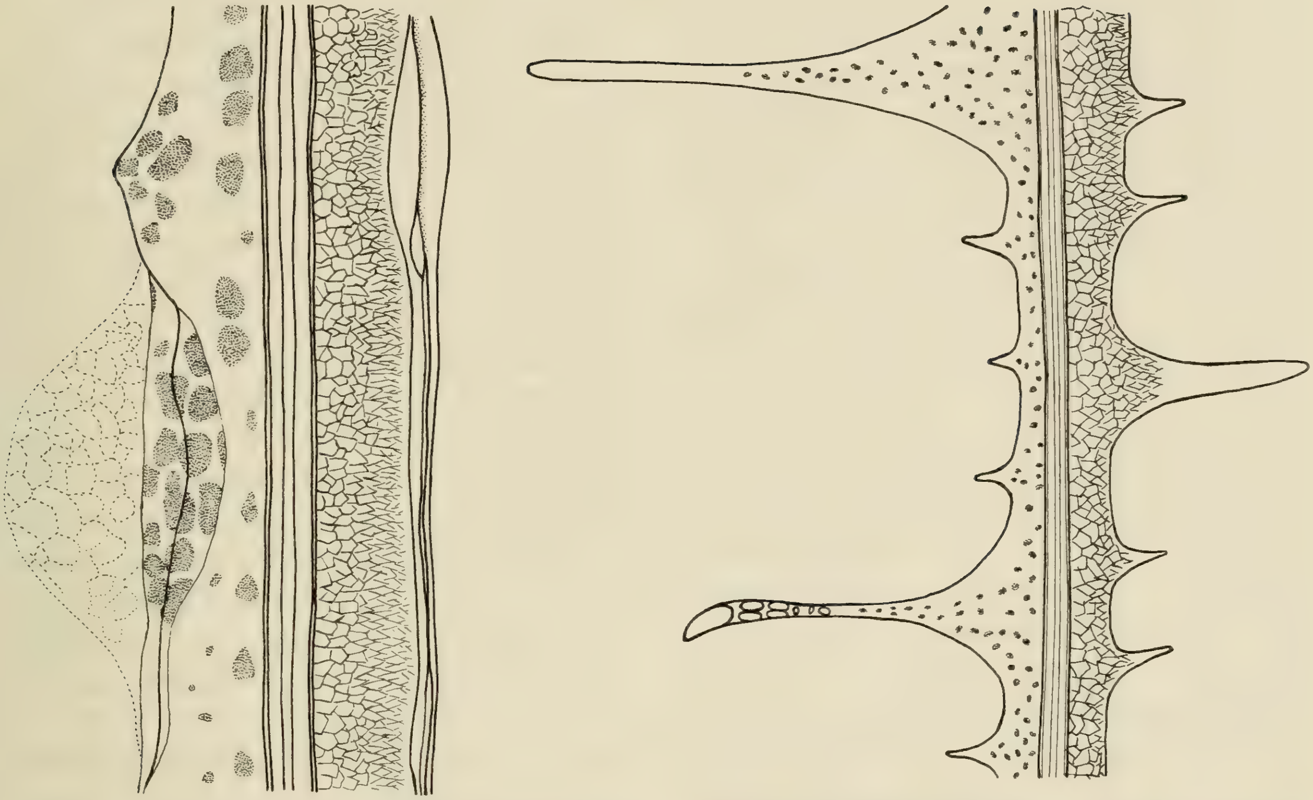

Fig. 2. Composite view of details of tail morphology. Left side of each figure shows chromatophore pattern, right side shows reticulation of tissue. (A, left) Pacific specimen, USNM 817761. In preserved specimens the edges of the tail are tightly rolled. Large stippled area on the left shows approximate shape and chromatophore pattern of deflated pouch when unrolled. (B, right) Atlantic specimen, USNM 817762. Positions of white (distal) and yellow (medial) bead-like structures seen in photographs of the live specimen are indicated on one large flap (lower left of B).

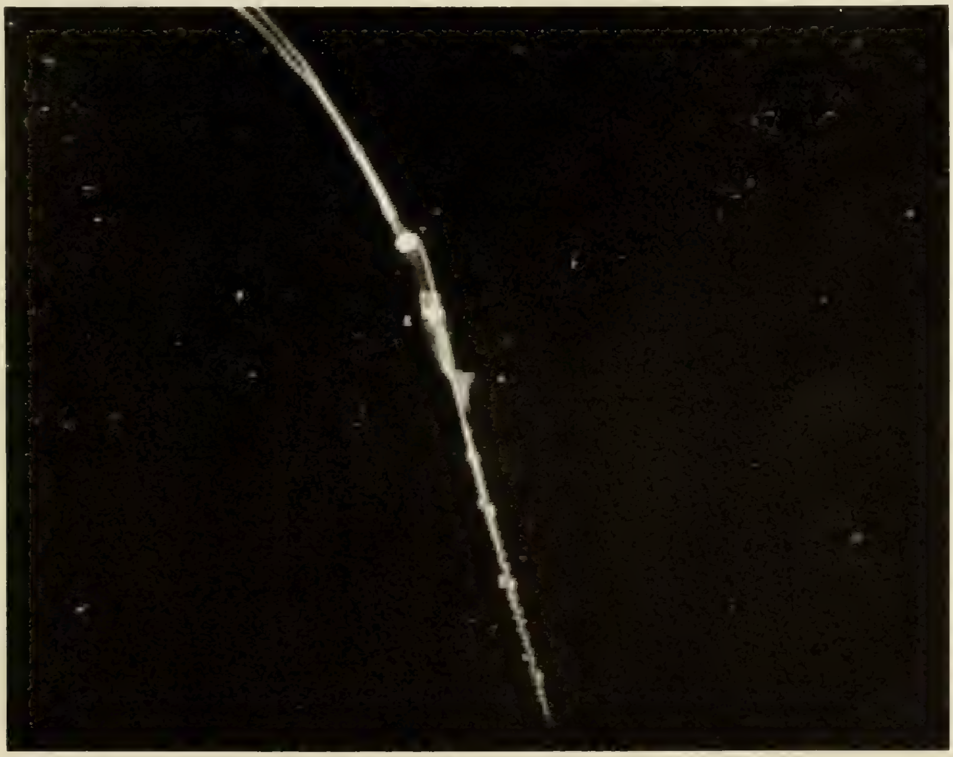

Fig. 3. Still frame from a videotape recorded in-situ, showing a Pacific doratopsis. The squid is oriented obliquely with the tail directed down and the arms and tentacles up.

in these midwater squids. Chromatophore displays observed on live animals aboard ship included: (1) a dark longitudinal stripe along the dorsal midline of the tail, mantle, neck, head, and arms; (2) progression of chromatophore expansion along the dorsal midline from arms toward tail; and (3) independent darkening of separate regions, such as the pouches, fins, tentacle tips, and the mantle in the vicinity of the digestive gland.

All doratopses were observed in-situ within the depth range of 278–471 m.

Atlantic specimen.—Material examined: 1 specimen collected, not videotaped but photographed alive in aquarium, 43 mm ML, depth 142 m, Oct 1979, "nighttime," "Bahamas," USNM 817762.

Description of animal (Fig. 1B): Tentacles thin but muscular, very long, longer than ventral arms, with suckers along distal half, tips sightly expanded as clubs with single dorsal keel, narrow trabecular membranes present along both sides of sucker-bearing distal half; no pads on aboral side along proximal half of tentacles; suckers tetraserial on tentacle stalks and clubs. Arms IV≫III>II>I; teeth could not be seen on sucker rings; tentacle sheaths on ventral arms well developed, of vesiculate tissue. Arm-crown pillar gelatinous and long, much longer than head length, strongly and coarsely vesiculate, forming chambers, esophagus located dorsally. Head short. Olfactory papillae well developed, finger-like, located ventrally, anterior to statocysts. Eyes egg-shaped in lateral view, with small end oriented anteroventrally. Neck long (ca. ⅓ ML), narrower than mantle, gelatinous, strongly and coarsely vesiculate, forming chambers. Digestive gland and gills located near base of funnel at anterior end of mantle cavity; bean-shaped. Ink sac embedded on ventral surface of digestive gland; no trace of photophores on digestive gland or ink sac. Mantle terminates posteriorly near anterior insertion of fins, very delicate integumentary tissue continues posteriorly from mantle end covering gladius ventral to fins. Tissue of posterior mantle finely vesiculated. Fins narrow, width less than length, oval except at anterior and posterior ends where muscular concavities are partly filled with delicate tissue. Chromatophores bleached in preserved specimen; large chromatophores yellow and smaller chromatophores red in photographs of live specimen; form pronounced stripe along dorsal midline of mantle, neck and arm-crown pillar; absent from ventral midline of mantle but present on ventral midline of arm-crown pillar; scattered around centers of ventral surface and entire dorsal surface of fins; on aboral surface of all arms; no chromatophores visible on tentacles but tentacles enclosed within tentacle sheaths of arms IV in photographs; patches of chromatophores on ventral and dorsal surfaces of head; chromatophores laterally on funnel and collar, at posterior end of mantle and on arm-crown pillar; band of small chromatophores around edge of anterior mantle opening; other chromatophores scattered dorsolaterally on mantle and neck.

Tail morphology (Fig. 2B): Tail long, longer than length of specimen from posterior edges of fins to tips of lateral arms, constricted near posterior border of fins, then broad throughout length. Posterior tip missing. Long, narrow, pointed flaps staggered along sides of tail, each separated by 4–6 shorter pointed flaps. In photographs of the live specimen, yellow and white bead-like structures, possibly fluid-filled pouches, were located at the tips of the long flaps; these structures cannot be seen in preserved specimen. Tissue of tail vesiculate, especially near central gladius. Gladius cross-section box-shaped with concave lateral walls, narrow open gap in ventral wall, and with dorsal-midline ridge. Chromatophores concentrated on soft integument along both sides of gladius and on central axes of flaps.

Behavior: This squid assumed the same posture in the shipboard aquarium as was observed in-situ for the Pacific specimens.

When the squid moved in the aquarium, it kept its digestive gland oriented vertically regardless of the orientation of the body axis. The fragility of the tail, which broke at its constriction near the fins during transfer from the sampler, also was similar to the Pacific specimens.

Discussion

Without a complete growth series, inferences about the species identity of these paralarvae of *Chiroteuthis* must be based on assumptions about the systematics and known species distributions within the genus. This is relatively simple for the Pacific specimens but much more complicated for the specimen from the Atlantic.

Chiroteuthis calyx Young, 1972 is the only species known from Californian waters. It is commonly caught in midwater trawls off northern California (Vecchione, unpublished data). Earlier reports of *C. veranyi* from California and Oregon actually represent *C. calyx* (see Young 1972), which is very similar to the Mediterranean/Atlantic *C. veranyi.* A doratopsis described by Berry (1963) was identified as *C. calyx* by Young (1972), as were two doratopses included in the original description of the species. Our Pacific specimens conform to these earlier descriptions of paralarvae. We are therefore confident that our specimens are *C. calyx.* Here we add details about the tail morphology to the description of that species. Intraspecific variation was quite small among our few specimens.

As we mentioned in the introduction, Ficalbi (1899), supported by Naef (1923), demonstrated that "Doratopsis vermicularis" is actually the paralarva of *C. veranyi.* One of Ficalbi's specimens had a fragment of the tail remaining, as did two of Pfeffer's (1912, plate 46) doratopses. Pfeffer's specimens, for which collection location was not presented, clearly represent two separate species of *Chiroteuthis.* Given differences in artistic style (Ficalbi's figures are comparatively crude), we believe that the specimen in Pfeffer's figures 1 and 2 belongs to the same species as Ficalbi's specimen, *C. veranyi.* All of these figures show indications of paired lateral pouches on the tail, similar to those described above for *C. calyx.* They also show a proximal constriction of the tail near the fins, as well as tissue expanded laterally from the gladius.

Young (1972) pointed out in the original description that *C. calyx* is very similar to *C. veranyi.* Likewise, strong similarities exist between the paralarvae of *C. calyx* and those of *C. veranyi* as described by Ficalbi (1899) and Pfeffer (1912). These similarities include chromatophore patterns, presence and location of lateral pouches on the tail, and the proximal constriction of the tail. The most noticeable difference between paralarvae of these species is the apparent lack of flaps (tissue lobes) between the pouches on the tail of paralarval *C. veranyi.*

Tail morphology of Pfeffer's other specimen (plate 46, figure 3) is very different from any other described specimens. It appears to have a broad oval pair of flaps about 1 ML from the fins, with no other lateral tissue apparent on the extended gladius of the tail. We cannot associate this specimen with any described species at this time.

The species of *Chiroteuthis* commonly reported from the western North Atlantic are *C. veranyi* and *C. lacertosa* Verrill, 1881 (*Leptoteuthis diaphana* Verrill, 1884 is a juvenile *C. lacertosa*). In addition, *C. joubini* Voss, 1967 and *C. capensis* Voss, 1967, originally described from the equatorial Atlantic and the eastern South Atlantic, respectively, recently have been found in the Gulf of Mexico (Passarella & Hopkins 1991). *Chiroteuthis lacertosa* is so similar to *C. veranyi,* differing only slightly in the shape of the fins and perhaps in details of the club, that their status as separate species is doubtful. The extreme differences between our Atlantic specimen and the *C. veranyi* doratopses of Ficalbi (1899) and Pfeffer (1912, plate 46, figures 1 and 2) convince us that our specimen is neither *C. veranyi* nor *C. lacertosa.*

Although less compelling, indirect evidence indicates that our specimen probably is not *C. joubini.* We have an early juvenile *Chiroteuthis,* similar to *C. joubini,* 50 mm ML, from the Gulf of Mexico that possesses rows of separate, bead-like ocular photophores, paired photophores on the digestive gland, and central expansions of the trabecular membranes on the clubs. These characters conform to specimens described by Nesis & Nikitina (1984) in a redescription of *C. joubini* which, based on present knowledge, probably represent an undescribed species. The Atlantic specimen reported here, 43 mm ML, shows no indication of any of these diagnostic characters. Whereas our 44-mm ML *C. calyx* has paired photophore rudiments on the digestive gland, none were seen on the 43-mm ML Atlantic specimen. Its ocular photophore rudiments appear to be similar to those of *C. calyx,* which develops a large strip of photogenic tissue on the ventral surface of the eye. The remaining *Chiroteuthis* species now known from the western North Atlantic, *C. capensis,* is characterized by strip-like ocular photophores, lack of photophores on the digestive gland, and lack of the expansion of the trabecular membrane. We therefore feel that our Atlantic specimen is more likely to be *C. capensis* than *C. joubini,* s.l. The possibility remains, though, that it is the paralarva of an undescribed species.

Other genera of Chiroteuthidae possess tails in the subadult/adult stages that are reminiscent of those of paralarval *Chiroteuthis.* These adult tails probably represent paedomorphy, the retention of ancestral larval characteristics in advanced developmental stages. The long tail of an undescribed genus that occurs in Hawaiian waters (R. E. Young, University of Hawaii, pers. comm.) is remarkably like that of paralarval *Chiroteuthis veranyi,* but it apparently lacks the fluid-filled pouches. On *Grimalditeuthis,* the gladius extends well posterior to the fins and supports a broad, heart-shaped structure that traditionally has been referred to as a "secondary fin." This probably is the source of speculation that the tails of doratopses support one or more secondary fins (e.g., Nesis 1987:241), a terminology that implies an active locomotor function for these structures. Our observations, both of in-situ behavior and of microscopic structure, revealed no muscular movement in any structure of the tail. We have therefore established the nomenclature used above, pouches and flaps, to describe these structures and we advocate their standard use in future studies. While "secondary fin" probably does not accurately describe the tail structure on *Grimalditeuthis* because it is not muscular, it also differs greatly from the pouches and flaps we describe above for doratopses and our terminology would not be appropriate for that structure. It may function as a floatation device and, if so, should be referred to as a float.

Currently, we can only speculate on the functions of the tail structures on paralarval *Chiroteuthis.* The fluid-filled pouches may provide positive buoyancy to counterbalance the weight of the extended gladius. However, the entire tail is filled with vesiculate tissue which is almost certainly buoyant, so the buoyancy contribution of the pouches remains uncertain. A variety of buoyancy mechanisms are known in cephalopods, including fluid-filled vesicles in the arms and bodies of adult chiroteuthids (Denton & Gilpin-Brown 1973). This interpretation is quite different from speculation by Ankel (1974) that the tail functions primarily as a weight to counterbalance the weight of the arms, allowing the center of gravity to match the center of buoyancy provided by the neck (Denton & Gilpin-Brown 1973). Ankel (1974) argued that the typical position of a doratopsis in the water is horizontal in spite of his photograph of a specimen in an aquarium oriented obliquely vertical with the head up.

Patches of chromatophores on mesopelagic cephalopods often serve to cover structures that are opaque or luminescent. The fluid in the pouches is not opaque, so the concentrations of chromatophores over them may indicate a capability of luminescence, although we have no direct evidence of this yet.

The tail doubles the length of the animal with minimal investment of protein resources, but at the cost of maneuverability. Long thin animals, vertically oriented, are common in the mesopelagic realm (personal observations). The tail also gives the squid a very peculiar appearance which may serve to conceal its identity. In midwater, concealment usually is achieved by attempts to be invisible (e.g., transparency, reflectivity, or bioluminescent counterillumination) or by mimicry. In doratopsis the tail may contribute to mimicry. While reviewing the in-situ videotapes of *C. calyx,* we were impressed with the similarity of its appearance to that of nearby mesopelagic siphonophores (*Nanomia bijuga*) which possess powerful nematocysts; the doratopsis tail pouches looked much like the nectophores and bracts on a siphonophore. The tail may also be important in the escape reaction, as it is almost always pointed downward and because the theoretical maximum velocity of a body through a fluid is proportional to its length. Regardless of its function while attached, the tail is unquestionably designed to detach easily from the animal. Possibly this serves a similar function to the autotomizing tail of a lizard. A predator may be distracted by the detached tail, possibly leaking luminscent fluid, while the squid escapes.

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NEW SPECIES AND RECORDS OF PHYLLODOCIDAE (POLYCHAETA) FROM THE CONTINENTAL SHELF AND SLOPE OFF CALIFORNIA

James A. Blake

Abstract.—Six new species of phyllodocid polychaetes are described from the continental shelf and slope off central California, mostly in vicinity of the Santa Maria Basin. New species include *Eteone brigitteae, E. leptotes, E. pigmentata, Lugia uschakovi, Protomystides mariaensis,* and *Sige pleijeli.* A redescription of *Sige brunnea* (Fauchald, 1972) is presented based upon new collections from off San Francisco.

In 1990, the U.S. Department of the Interior, Minerals Management Service (MMS), initiated a project to prepare a taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. These areas and other locations on the California continental shelf have been the site of extensive biological reconnaissance and monitoring programs that were conducted to assess the environmental resources prior to the exploration and/or development of oil and gas reserves. One of the largest polychaete families being treated in the atlas is the Phyllodocidae, where 27 species distributed in 12 genera are described and illustrated (Blake 1992). Six of these species are new to science and their descriptions are presented here. In addition, a redescription of *Sige brunnea* (Fauchald, 1972) is presented so that one of the new species, *Sige pleijeli* can be clearly distinguished. Positions and depths for the Santa Maria Basin stations are presented in Table 1. The type specimens are lodged in the National Museum of Natural History (USNM), the Los Angeles County Museum of Natural History (LACM-AHF), and Santa Barbara Museum of Natural History (SBMNH).

Systematic Account

Genus *Eteone* Savigny, 1822

Diagnosis.—Prostomium with 4 antennae; nuchal papilla present or absent; 2 pairs of tentacular cirri on first segment; second segment lacking dorsal cirri. Proboscis smooth or rugose, lacking longitudinal rows of papillae. Anal cirri short, globular to digitiform with rounded tips, no more than 4 times longer than wide.

Remarks.—*Eteone* was revised by Wilson (1988) to include three genera: *Eteone, Hypereteone* Bergström, and *Mysta* Malmgren. The genera were separated on the form of the anal cirri and the presence and location of papillae on the proboscis. *Hypereteone* was distinguished by having long tapering anal cirri that were three times as long as wide and three or more rows of papillae or heavy ridges on the proboscis. Both *Eteone* and *Mysta* were said to have short anal cirri with rounded tips. *Mysta* was distinguished from *Eteone* by having two lateral rows of papillae on the proboscis, whereas *Eteone* lacked such rows. While it is apparent that three distinct groups of species can be separated within the *Eteone*-complex of species, Pleijel (1991) did not recognize these taxa at the generic level. He was concerned that *Eteone* sensu stricto, might represent a paraphyletic assemblage defined on plesiomorphic characters. I also have doubts that three genera should be recognized. *Eteone brigitteae,* newly described in the present study (see below), has asymmetrical dorsal cirri, and is most closely allied with species that are included with *Hypereteone* (Wilson 1988). However, the anal

Table 1.—Location of soft-substrate stations in the Santa Maria Basin cited in this paper.

Station	Latitude (N)	Longitude (W)	Depth (m)
12	35°15.03′	120°57.31′	98
13	35°14.54′	120°59.77′	197
56	34°30.32′	121°01.02′	900
R-1	35°05.83′	120°49.16′	91
R-4	34°43.01′	120°47.39′	92
R-7	34°52.90′	121°10.30′	565
R-8	34°55.30′	120°45.87′	90
PJ-1	34°55.79′	120°49.91′	145
PJ-2	34°55.32′	120°49.59′	142
PJ-4	34°56.26′	120°50.24′	150
PJ-5	34°55.32′	120°50.24′	152
PJ-7	34°55.79′	120°48.60′	123
PJ-8	34°56.87′	120°49.91′	142
PJ-10	34°53.63′	120°49.91′	147
PJ-17	34°56.56′	120°48.98′	126

cirri of *E. brigitteae,* while elongate, are thick and blunt-tipped instead of tapering to a point. With these reservations in mind, I prefer to follow Pleijel (1991) in treating *Hypereteone* and *Mysta* as junior synonyms of *Eteone.*

Eteone brigitteae, new species
Fig. 1

Material examined.—California: Santa Maria Basin, off Point Sal, Sta. R-8 (holotype and paratype USNM 148680-148681).—Off San Francisco, EPA Sta. 3-12, 37°25.03′N, 123°18.00′W, 1745 m, coll. Sep 1991, 1 specimen.

Description.—A moderate sized species, up to 20.5 mm long and 0.6 mm wide anteriorly, for about 140 segments. Color in alcohol: light tan, relatively unpigmented except for some brown spots along dorsal midline. Prostomium slightly longer than wide, tapering abruptly about mid-way to anterior end, then expanding again, terminating in bluntly rounded tip bearing 4 short cirriform antennae (Fig. 1A); with one pair of dark eyes present in Santa Maria Basin specimens, lacking in San Francisco slope specimen; nuchal papilla absent.

Tentacular segment weakly separated from prostomium (Fig. 1A). Dorsal tentacular cirri short, extending posteriorly only to anterior of segment 2; second pair longer, extending to segment 3 (Fig. 1A). Second segment with setae and ventral cirrus. Each dorsal cirrus asymmetrical, especially in anterior segments, where dorsal edge curves and ventral edge is relatively straight (Fig. 1B); middle dorsal cirri longer, with less extreme asymmetry (Fig. 1C). Ventral cirri elongate, with broad basal attachment; ventral cirri of anterior segments nearly as long as podial lobes. Podial lobes with weakly developed anterior and posterior lobes, between which setae emerge. Setae number 9 to 10 per fascicle; each with finely denticulated blade and shaft with a single large rostral tooth and shorter double spike; larger tooth with several smaller teeth around base (Fig. 1D–F). Pygidium with 2 thick, elongated anal cirri, with blunt tips, each about 2.25 times as long as wide (Fig. 1G).

Remarks.—*Eteone brigitteae* is closely related to *E. fauchaldi* Kravitz & Jones (1979) from off Oregon and Washington in shelf depths, and *E. aestuarina* Hartmann-Schröder (1959) from El Salvador in shallow water estuarine habitats. All three species have elongate pygidial anal cirri, setae from segment 2, a prostomium that is longer than wide, and dorsal cirri that are more or less asymmetrical in shape. In *E. fauchaldi,* the ventral tentacular cirri are only slightly longer than the dorsal, while both *E. brigitteae* and *E. aestuarina* have ventral tentacular cirri that are at least twice as long as the dorsal. The dorsal cirri are only vaguely asymmetrical in *E. fauchaldi,* but are strongly asymmetrical in *E. brigitteae* and *E. aestuarina. E. brigitteae* differs from both *E. fauchaldi* and *E. aestuarina* in having thick, robust anal cirri that end in blunt tips instead of ones that are long, tapering, and end in pointed tips. *E. brigitteae* is also similar to *E. heteropoda* Hartman, 1951 from the eastern and Gulf coasts of the United States in having asymmetrical dor-

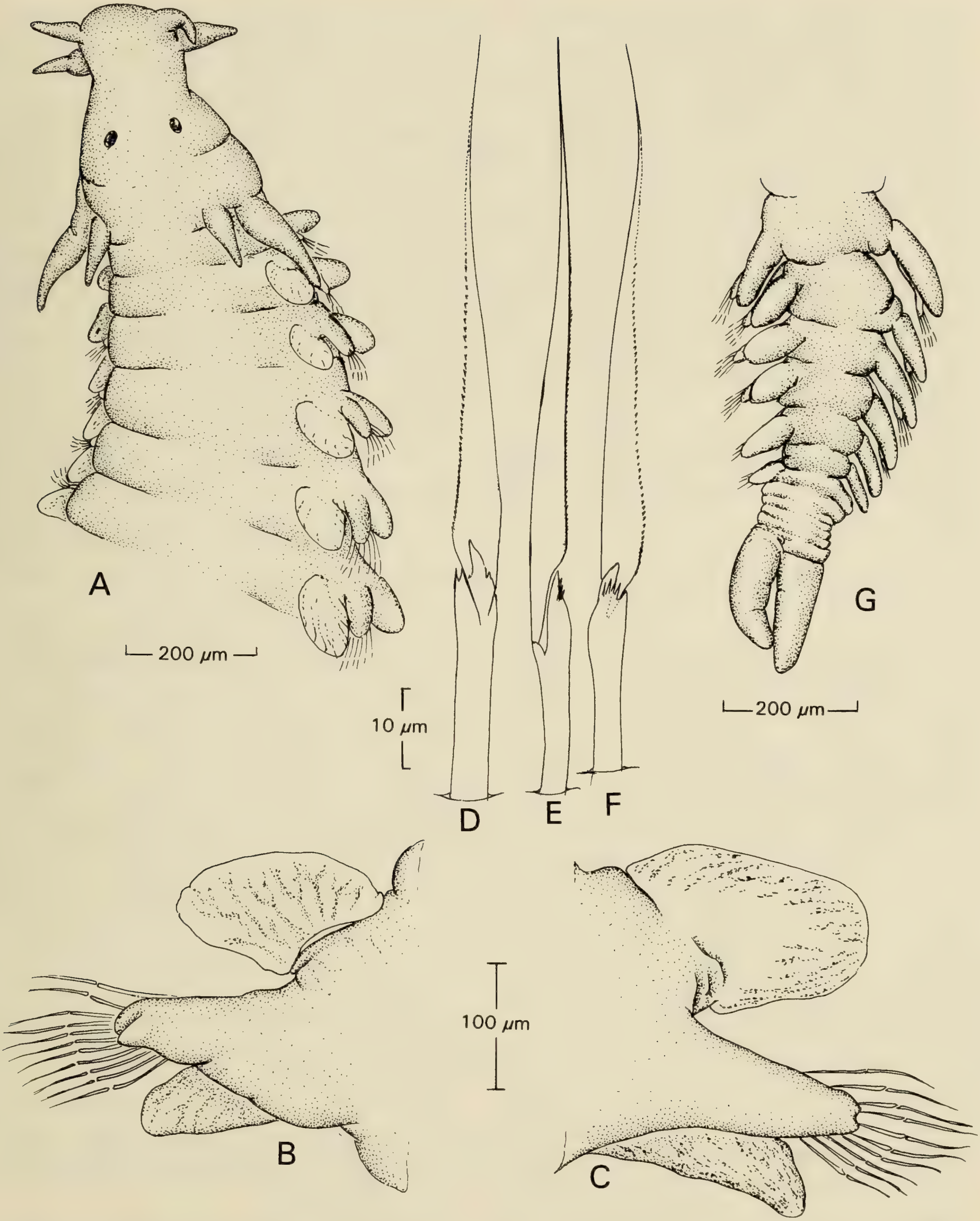

Fig. 1. *Eteone brigitteae* (USNM 148680): A, Anterior end, dorsolateral view; B, anterior parapodium, anterior view; C, middle parapodium, anterior view; D–F, setae in various views; G, posterior end, dorsal view.

sal cirri. However, in *E. heteropoda* the prostomium is distinctly wider than long instead of longer than wide, the dorsal cirri are pointed instead of broadly rounded, and the anal cirri are long and tapering instead of blunt-tipped. Specimens of *E. brigitteae* from the continental shelf (Santa Maria Basin) are indistinguishable from the specimen from the continental slope off San Francisco, except for the presence of a single pair of small eyes in the former.

Etymology.—This species is named for Dr. Brigitte Hilbig, polychaete systematist, friend, and colleague.

Distribution.—Known only from the Santa Maria Basin, in sediments having high silt content, 90 m; off San Francisco in slope depths, 1745 m.

Eteone leptotes, new species
Fig. 2

Material examined.—California: Santa Maria Basin, Sta. PJ-2 (holotype and 2 paratypes, USNM 148682-148683), PJ-7 (3 paratypes USNM 148684), PJ-8 (2 paratypes USNM 148685), PJ-10 (1 paratype LACM-AHF POLY 1607), PJ-17 (13 paratypes LACM-AHF POLY 1608), R-1 (11 paratypes SBMNH 35615) R-4 (2 paratypes LACM-AHF POLY 1609), R-7 (1 paratype, LACM-AHF POLY 1610), R-8 (100+ paratypes USNM 148686-148692).

Description.—A small, thin, threadlike species; holotype 2.8 mm long and 0.16 mm wide anteriorly for 32 setigers; paratypes up to 6.3 mm long and 0.3 mm wide for 90 setigers. Color in alcohol: white to light brown with dark brown pigment organized in distinctive pattern; pigment concentrated in individual granules or spots concentrated on dorsum, ventrum, dorsal cirri, and anal cirri.

Prostomium and first segment fused, sometimes with notch at border of tentacular segment; prostomium narrowing abruptly anterior to eyes, then tapering to rounded tip, bearing 4 subequal antennae (Fig. 2A–B); 2 dark red eyes present at border of prostomium and peristomium; each eye with clear lens surrounded by dark red pigment; nuchal papilla located posterior to eyes. Proboscis entirely smooth. Tentacular cirri short, subequal (Fig. 2A–B). Second segment bearing prominent podial lobe with setae and ventral cirrus. Each dorsal cirrus thickened, distally rounded, becoming longer, somewhat lanceolate in middle body segments (Fig. 2C); dorsal cirri of anterior and posterior segments as long as or shorter than podial lobe, in middle body segments slightly longer than podial lobe (Fig. 2C). Ventral cirri short, non-pigmented, never longer than podial lobe (Fig. 2C).

Setae numbering 4 to 6 per fascicle; all compound spinigers with expanded tip of shaft bearing 2 prongs, covered with fine spinelets (Fig. 2E–F); blade with serrated cutting edge. Pygidium bearing two short, thick anal cirri (Fig. 2D).

Remarks.—*Eteone leptotes* is most closely related to *E. filiformis* Hartmann-Schröder, described from Western Australia in 1980. Both are minute, threadlike forms, and entirely different in this regard from other known species. *Eteone leptotes* differs from *E. filiformis* in having subequal tentacular cirri instead of dorsal ones that are longer. *Eteone filiformis* appears to attain a larger size than *E. leptotes* because the three specimens described by Hartmann-Schröder (1980) are about twice as long and have more than twice as many setigers. Locally, this species was identified as *Eteone* sp. E in the MMS monitoring programs in the Santa Maria Basin.

Etymology.—The epithet is derived from the Greek, *leptos,* for thin or slender, referring to the slender, threadlike nature of the body of this worm.

Distribution.—Central California continental shelf, 90–150 m.

Eteone pigmentata, new species
Fig. 3

Material examined.—California: Santa Maria Basin, Sta. PJ-7 (holotype, USNM

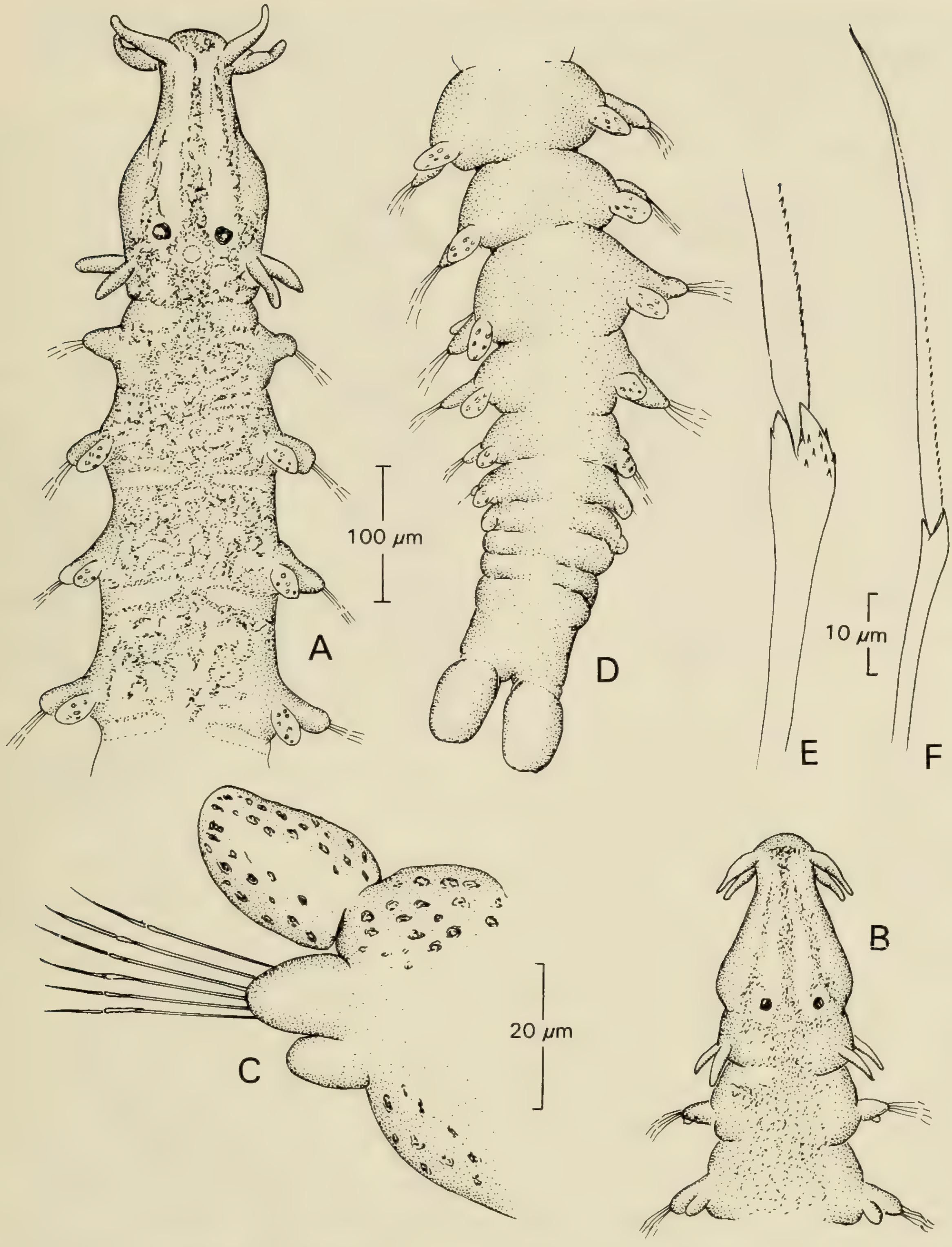

Fig. 2. *Eteone leptotes* (USNM 148686-92): A–B, anterior ends of different specimens, dorsal view; C, middle parapodium; D, posterior end, dorsal view; E–F, setae [B, same scale as A and D; E, not to scale].

148693), R-1, paratype (SBMNH 35616), R-8 (4 paratypes, LACM-AHF POLY 1611, 1620–22), 12 (paratype, USNM 148694).

Description.—A large robust species; holotype 28 mm long, 0.8 mm wide anteriorly for 110 setigerous segments; paratype (USNM 148694) 18 mm long, 0.8 mm wide for 74 setigers and regenerating posterior portion. Color in alcohol: light brown with very dark brown to black pigment on segmental rings of anterior segments, dorsal and ventral cirri, podial lobes, anal cirri, and some lighter concentrations on prostomium; middle and posterior segments with less pigment; dark pigment concentrated in dense aggregations of small granules.

Prostomium and tentacular segment clearly separated by lateral furrow (Fig. 3A); prostomium about 1.5 times as wide as long, tapering abruptly from widest posterior portion to narrow anterior end; 4 antennae attached to expanded, rounded anterior tip; 2 subsurface eyes present, inconspicuous, each with lens and pigment cup. Small rounded nuchal papilla present posterior to eyes. Dorsal tentacular cirri slightly longer than ventral, extending posteriorly to anterior border of setiger 3 (Fig. 3A). In dissection, proboscis appearing smooth. Second segment bearing well-developed podial lobe with setae and ventral cirrus. Dorsal cirri first present from setiger 2; each dorsal cirrus thickened, inflated, oval, about as long as podial lobes (Fig. 3B); ventral cirri similar to dorsal, but with broader basal attachment.

Setae numbering about 10 per fascicle, all compound spinigers with expanded tip bearing 4 to 5 long prongs (Fig. 3D–F); blade with very fine dentition along cutting edge. Pygidium bearing two short, thickened anal cirri (Fig. 3C).

Remarks.—*Eteone pigmentata* appears to be closely related to *E. spilotus* Kravitz & Jones, 1979 described from shelf depths off the Columbia River, Oregon and Washington. Both species are darkly pigmented and have similarly shaped dorsal cirri. *E. pigmentata,* however, has a prostomium that is clearly wider than long, ventral cirri that are as long as the podial lobe, and dorsal tentacular cirri that are slightly longer than the ventral ones, whereas the prostomium of *E. spilotus* is longer than wide, the ventral cirri are always shorter than the podial lobe, and the tentacular cirri are subequal. The setae of *E. spilotus* were described by Wilson (1988) and found to have four large teeth on the end of the shaft and several smaller ones. This arrangement was unique among the species of *Eteone* that he studied. Very similar setae are present in *E. pigmentata,* thus emphasizing the close similarity of these two species.

Etymology.—The species name, *pigmentata,* is derived from the Latin, *pigmentum,* referring to the conspicuously colored body.

Distribution.—Central California continental shelf, 90–150 m.

Genus *Lugia* Quatrefages, 1866

Diagnosis.—Prostomium with 4 antennae; median antenna and nuchal papilla lacking. One pair of tentacular cirri on first segment, setae absent; second segment with 1 pair dorsal tentacular cirri, normal ventral cirrus or cirrus only slightly larger than normal, and setae; third segment with normal dorsal and ventral cirri; tentacular formula: $1 + S^1/_v + S^D/_v$ or $0^1/_0 + S^1/_1 + S^D/_v$. Proboscis with soft papillae. Tentacular segments more or less free from one another and from prostomium.

Remarks.—Five species of the genus *Lugia* have been described: *L. pterophora* (Ehlers, 1864) from the Mediterranean, *L. abyssicola* Uschakov (1972) from deep water off Japan and California, *L. incognita* Campoy & Alquezar (1982) from off Spain, and *L. atlantica* Villalba & Viétez (1988), also from Spain; *Lugia rarica* Uschakov (1958) from off Kamchatka has been referred to *Mystides* by Uschakov (1972). Pleijel (1991), as part of review of benthic Phyllodicidae, reviewed the species assigned to *Lugia* and determined that the types of *L. incognita* and *L. atlantica* were both juveniles of *Eulalia.* He also considered that the type species, *L. pterophora,* was *nomina dubia* because no type material was available. Pleijel (1991) noted that *L. abyssicola* was the only known species of the genus that had the tentacular characters that agreed with the original generic diagnosis. Pleijel (1991) treated the genus *Lugia* as *nomina dubia.*

A new species that agrees fully with the

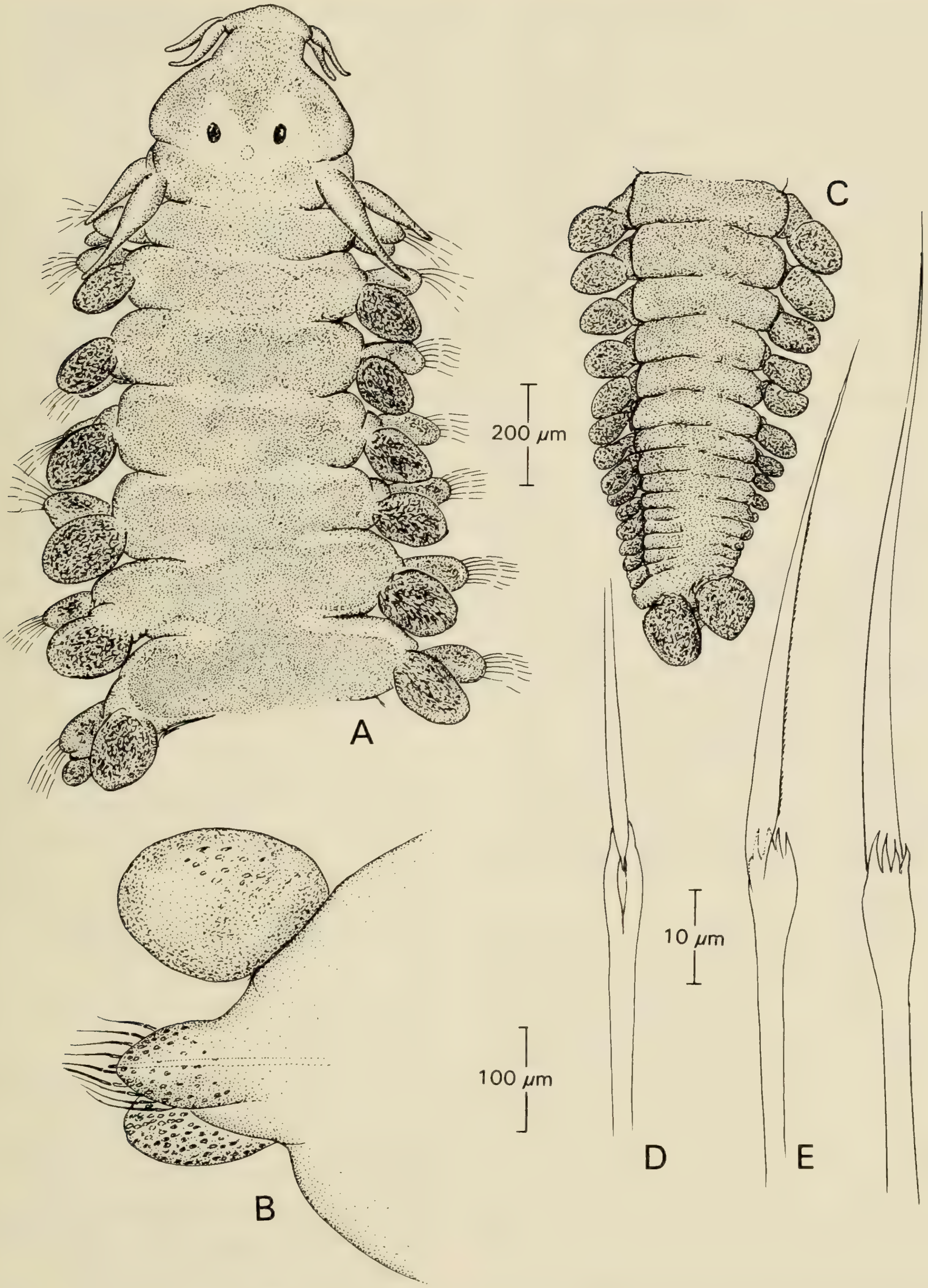

Fig. 3. *Eteone pigmentata* (USNM 148693): A, anterior end, dorsal view; B, middle parapodium, anterior view; C, posterior end, dorsal view; D–F, setae in different views.

generic diagnosis of *Lugia* has been discovered in the Santa Maria Basin. The generic diagnosis presented here follows that of Uschakov (1972) and is retained because both Uschakov's species, *L. abyssicola* and the new species, *L. uschakovi* agree with the definition. The status of the type species, *L. pterophora,* is not known and it will be necessary to collect new specimens from the type-locality before the status of the genus *Lugia* can be fully assessed.

Lugia uschakovi, new species

Fig. 4

Material examined.—California: Santa Maria Basin, Sta. PJ-1 (paratype, USNM 148695), PJ-5 (paratype, USNM 148696), PJ-7 (3 paratypes, LACM-AHF POLY 1612), PJ-8 (holotype, USNM 148697; paratypes LACM-AHF POLY 1613), PJ-10 (paratype, LACM-AHF POLY 1614), R-4 (4 paratypes, SBMNH 35613 and 35614), R-8 (2 paratypes, USNM 148698).

Description.—A small species, up to 5 mm long, 0.2 mm wide anteriorly, for about 65 setigers. Color in alcohol: light tan with brown specks on prostomium, body, and dorsal and ventral cirri.

Prostomium longer than wide, tapering anteriorly to slightly expanded apex bearing 4 short, cirriform antennae (Fig. 4A–B); eyes lacking; proboscis not observed. First segment only weakly distinguished from prostomium dorsally and ventrally, bearing a single pair of short, cirriform tentacular cirri; segment 2 first setigerous, with short podial lobe, short, cirriform dorsal tentacular cirrus and short lamellate ventral tentacular cirrus about 1½ times the length of normal ventral cirri on subsequent segments (Fig. 4B); segment 3 with normal dorsal and ventral cirri; tentacular formula: $0^1/_0 + S^1/_1 + S^D/_v$. Dorsal cirri short, conical, glandular, becoming larger in middle body segments (Fig. 4D); ventral cirri conical, about one-half the size of dorsal cirri (Fig. 4D). Setae arranged in spreading fascicle of 5 to 7 compound spinigers; each spiniger with broad blade bearing conspicuous denticles on cutting edge; tip of shaft with two rostral teeth, each with numerous fine denticles (Fig. 4E). Pygidium with 2 narrow, blunt-tipped anal cirri (Fig. 4C).

Remarks.—*Lugia uschakovi* from the continental shelf off California, most closely resembles *L. abyssicola* Uschakov from deep water off Japan and California in having an elongated prostomium that lacks eyes. The two species are most readily distinguished from one another by the form and length of the tentacular cirri. In *L. uschakovi* the dorsal tentacular cirri of segments 1 and 2 are both short, cirriform and of the same length. In contrast, the dorsal tentacular cirri of segment 2 in *L. abyssicola* are about 1½ times as long as that of the first segment. Further, the ventral tentacular cirrus of segment 2 in *L. uschakovi* is narrow and elongate instead of leaf-shaped.

Etymology.—This species is named for the late Professor P. V. Uschakov, Akademician of the Zoological Institute, Academy of Sciences, Leningrad, Russia, in recognition of his monographic work on the Phyllodocidae.

Distribution.—California continental shelf, in sand and silt, 90–150 m.

Genus *Protomystides* Czerniavsky, 1882

Diagnosis.—Prostomium with 4 antennae; elongate or rounded, nuchal papilla lacking; eyes present or absent; proboscis with soft papillae. All 3 tentacular segments distinctly separated from one another and prostomium; setae present from second segment. Tentacular cirri numbering 3 or 4 pairs of tentacular cirri on first 3 segments; tentacular formulae: $1 + S^1/_v + S^1/_v$ or $0^1/_0 + S^1/_1 + S^1/_v$.

Remarks.—Most of the known species of *Protomystides* are found in continental shelf or slope environments (Hartmann-Schröder 1963) and several are known from the deep sea (Uschakov 1972, Blake & Hilbig

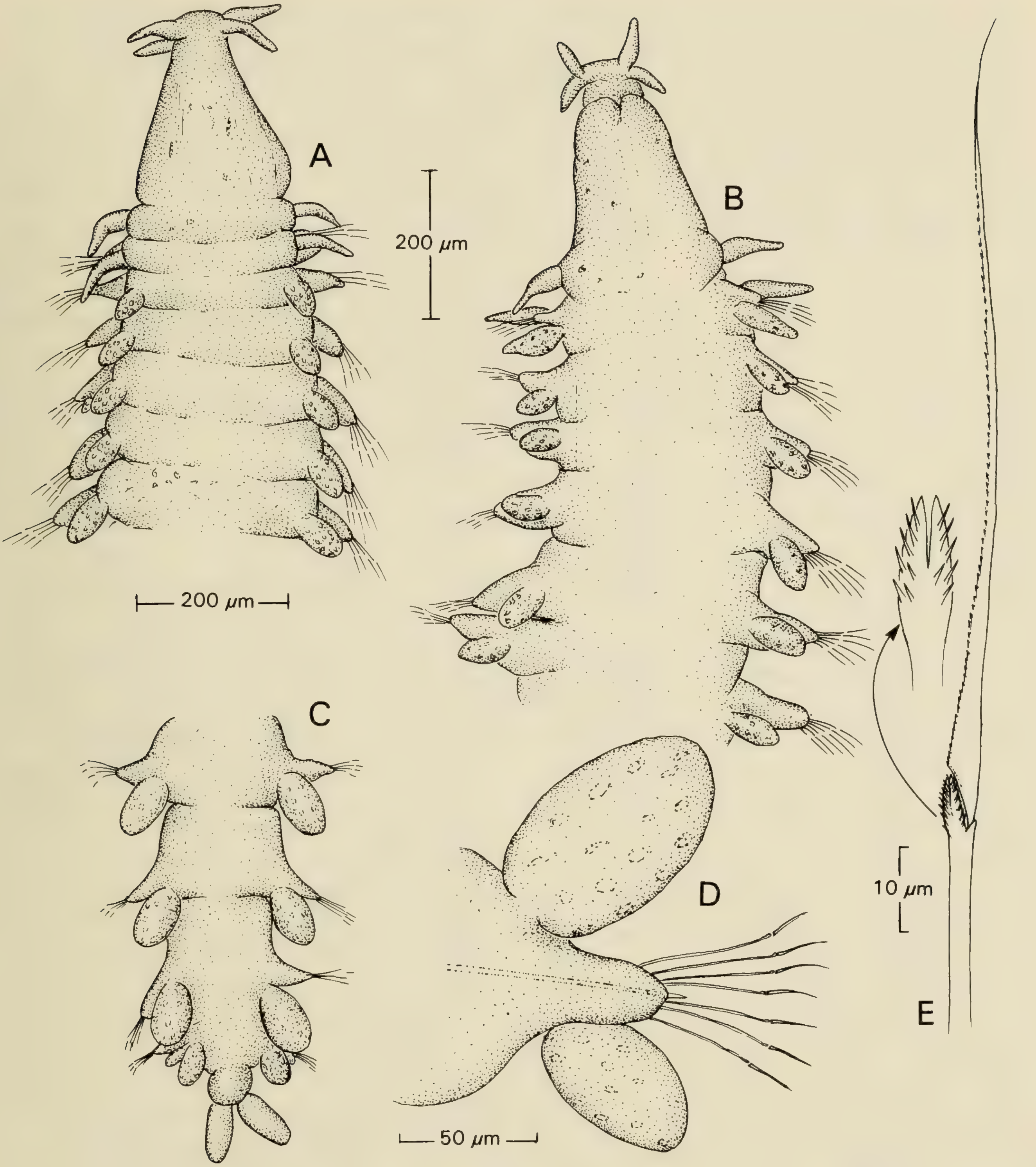

Fig. 4. *Lugia uschakovi* (USNM 148697): A, anterior end, dorsal view; B, same, ventral view; C, posterior end, dorsal view; D, middle parapodium, anterior view; E, seta [inset not to scale].

1990, Blake, unpublished). Plejel (1991) moved some species to *Eulalia* because nuchal papillae were found that corresponded to a medial tentacle. There have been few reports of the genus from North America. No species of *Protomystides* were recorded by Hartman (1968) in her Atlas of California polychaetes. In a survey of the continental slope off the U.S. Atlantic coast, three undescribed species of *Protomystides* have been discovered (Blake, unpublished); one new species has been discovered at the deep-sea methane seep community on the Florida Escarpment and at least two undescribed species have been discovered in lower slope depths off northern California in surveys conducted during the summers of 1990 and 1991 (Blake, unpublished). Another undescribed species has been discovered in the Santa Maria Basin and is here described.

Protomystides mariaensis, new species
Fig. 5

Material examined.—California: Santa Maria Basin, off Point Buchon, Sta. 13 (holotype, USNM 148700).

Description.—A small, slender species, 11.7 mm long 0.32 mm wide anteriorly for 96 segments. Color in alcohol: light tan with dark reddish, brown pigment on dorsal and ventral cirri and on anal cirri.

Prostomium slightly longer than wide, rounded anteriorly, bearing 4 frontal antennae on elevated cushion (Fig. 5A–B); with pair of dark eyes; no nuchal papilla apparent (Fig. 5A). Segments 1 to 3 distinct, set off from one another and from prostomium; dorsal tentacular cirri of segments 1 and 2 elongate, cylindrical, tapering; ventral tentacular cirri of segment 2 broad, somewhat flattened, tapering, about 3 times larger than normal ventral cirrus (Fig. 5A–B); tentacular formula: $1 + S^{1}/_{1} + S^{1}/_{v}$. Neuropodia short, rounded on tip, with fascicle of 6 to 8 compound setae; dorsal cirri thickened, oval, on basal cirrophore (Fig. 5C); ventral cirri smaller, elongate, rounded on tip (Fig. 5C). Setae with a large spike and numerous minute spinelets on tip of shaft (Fig. 5E–F). Anal cirri thick, with blunt tip, about 2½ times as long as broad (Fig. 5D).

Remarks.—*Protomystides mariaensis* is similar to *P. bilineata* La Greca (1947) from the Mediterranean in having an enlarged ventral tentacular cirrus on segment 2, in having eyes, and in having a prostomium that is slightly longer than wide. *Protomystides bilineata* was redescribed by Hartmann-Schröder (1963). *Protomystides mariaensis* differs from *P. bilineata* in having the body uniformly pigmented with small dark granules including very darkly pigmented dorsal, ventral, and anal cirri instead of two distinctive dark lines of pigment that extend from segment 3 down along the dorsal surface of the body. Furthermore, the dorsal cirrus of *P. bilineata* is relatively short, only as long as or slightly longer than the neuropodium, whereas in *P. mariaensis,* the dorsal cirrus is a large structure, extending for at least one-half of its total length beyond the neuropodium.

Etymology.—The species name is taken from the Santa Maria Basin where it was collected.

Distribution.—Known only from the Santa Maria Basin, in sediment with 85% silt, 197 m.

Genus *Sige* Malmgren, 1865

Diagnosis.—Prostomium pentagonal, with nuchal organs as posterior outgrowths; with 5 antennae; proboscis with numerous, mostly small papillae. Segment 1 fully developed, or reduced; with 4 pairs of tentacular cirri; ventral tentacular cirri of segment 2 cylindrical or slightly flattened; setae from segment 2; tentacular formula: $1 + S^{1}/_{1} + S^{1}/_{v}$. Parapodia uniramous, with dorsal and ventral cirri pointed; presetal dorsal lobe of parapodia distinctly prolonged, digitiform. Rostrum of setal shaft with large number of teeth, slightly decreasing in size proximally.

Remarks.—The genus *Sige* was redefined and revised by Pleijel (1990). *Sige* differs from all other described phyllodocids having five antennae by the nature of the prolonged superior neuropodial lobes. A similar character occurs independently in *Phyllodoce longipes* Kinberg, 1866.

Sige brunnea (Fauchald, 1972)
Fig. 6

Pirakia brunnea Fauchald, 1972:53–54, pl. 4, figs. C–D.
Sige brunnea: Pleijel, 1990:169–170, fig. 4.

Material examined.—California: the continental slope off San Francisco, Gulf of the

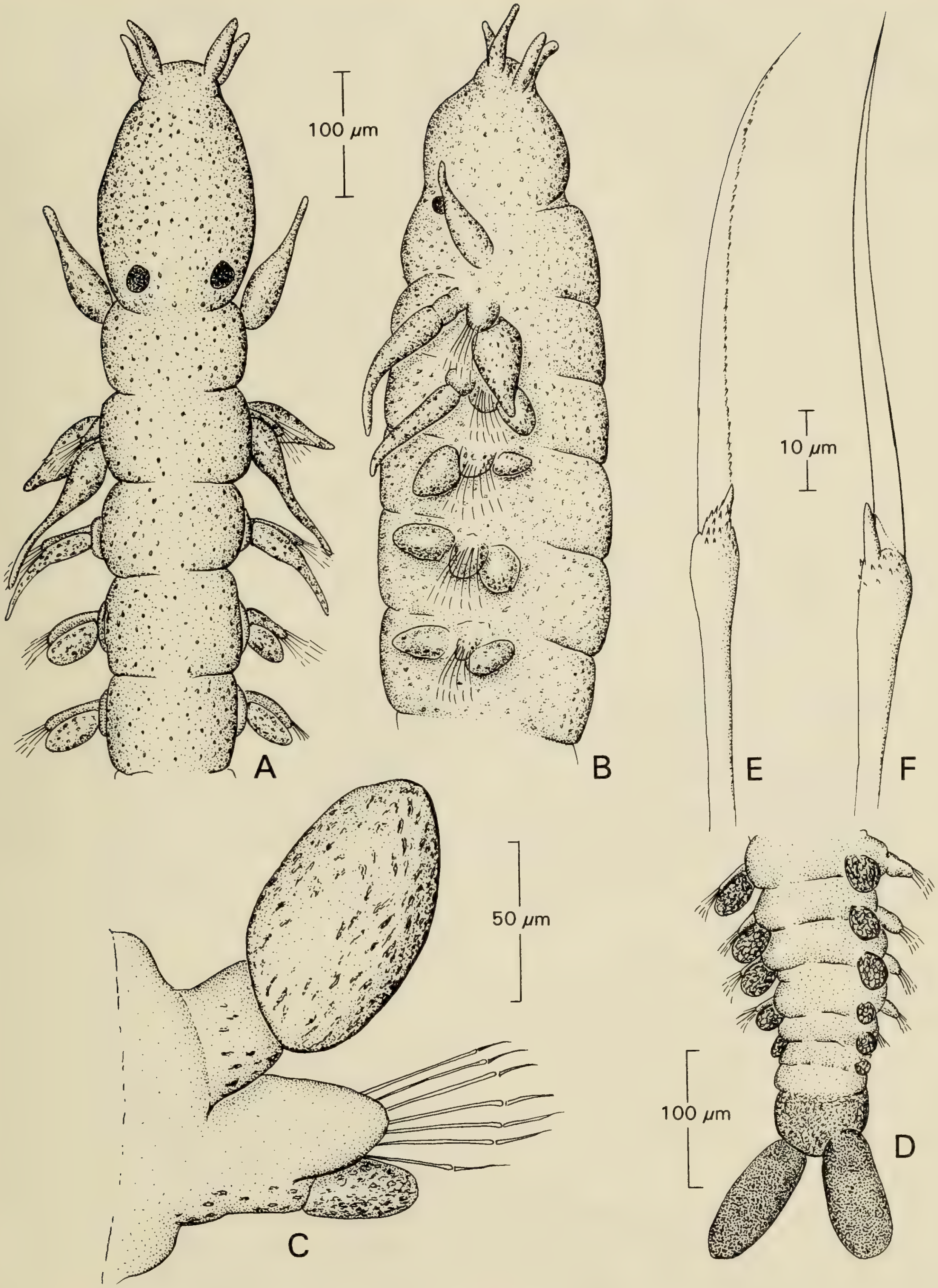

Fig. 5. *Protomystides mariaense* (USNM 148700): A, anterior end, dorsal view; B, same, lateral view; C, middle parapodium; D, posterior end, dorsal view; E–F, setae.

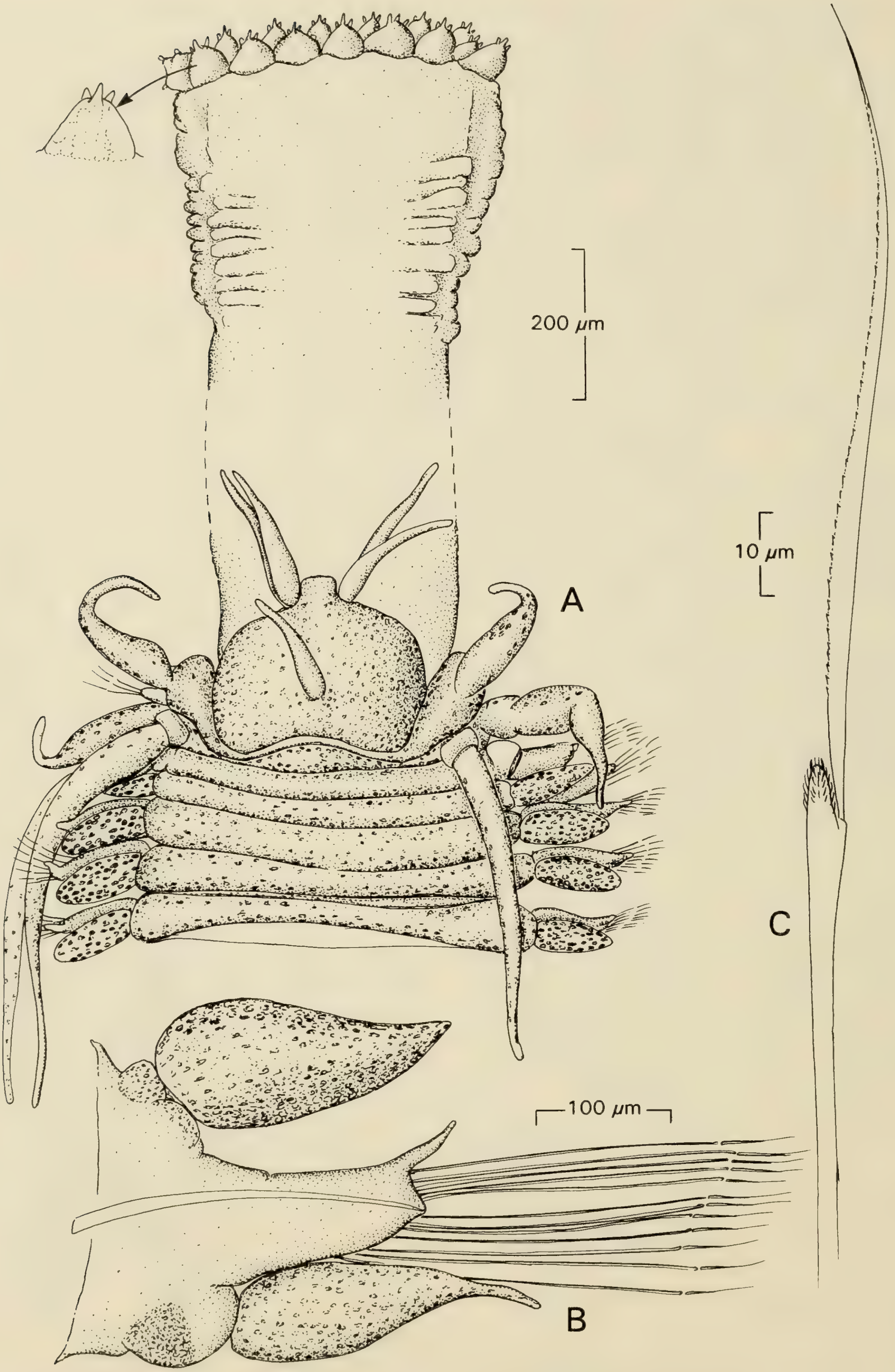

Fig. 6. *Sige brunnea* (Northern California specimen). A, anterior end, dorsal view; B, middle parapodium, anterior view; C, seta.

Farallones, 57 specimens from 12 stations in depths ranging from 1110–2955 m.

Description.—Northern California specimens mostly small, juveniles, with 14–18 segments, up to 2.0 mm long and 0.5 mm wide; 1 incomplete specimen, with 17 segments, 3.2 mm long and 0.8 mm wide; largest specimens 7–8 mm long and 1 mm wide with 42–45 segments; type specimen from Baja, California 10 mm long with 52 setigers (Fauchald 1972). Color in alcohol: tan with heavy concentrations of orange-brown pigment on prostomium, dorsal and ventral cirri, and on anterior and posterior margins of individual segments.

Prostomium wider than long, with prominent anterior projection arising between bases of frontal antennae; frontal antennae cirriform, subequal; median antenna shorter and more delicate than frontal antennae, arising from posterior one-third of prostomium (Fig. 6A). Proboscis smooth proximally, rugose distally with transverse ridges; terminal opening surrounded by 15–16 conical papillae (Fig. 6B), each with 3 projecting micropapillae; posterior margin of prostomium with broad, deep indentation.

All 3 tentacular segments complete and visible dorsally; first segment reduced, narrow dorsally; tentacular cirri all cylindrical, expanded basally, tapering apically; dorsal tentacular cirrus of segment 1 and ventral tentacular cirrus of segment 2 short, only extending posteriorly 2–3 segments; dorsal tentacular cirri of segments 2 and 3 longest, extending posteriorly 6–8 segments (Fig. 6A). Neuropodia with prominent, fingerlike superior lobe; dorsal cirri flattened, expanded basally, tapering apically to relatively sharp point; ventral cirrus more cirriform and elongate than dorsal cirri, extending for about one-third length beyond neuropodium (Fig. 6B). Setae numbering 12–20 per fascicle; each with thick, rounded rostrum on shaft bearing numerous small denticles; blade elongate, with serrated edge (Fig. 6C). Pygidium a rounded lobe; anal cirri not apparent.

Remarks.—*Sige brunnea* was originally described from deep water off western Mexico (Fauchald 1972) and has subsequently been reported from deep basins off southern California. The species is the most abundant phyllodocid in the lower slope benthos off northern California. It is most closely related to *S. pleijeli* in having elongate, tapering dorsal and ventral cirri. The two species differ most conspicuously in that the median antenna of *S. brunnea* is located in the posterior one-third of the prostomium, whereas, it is located anteriorly on the prostomium of *S. pleijeli.* In addition, the tentacular cirri of *S. pleijeli* are all short, never extending more than 2 segments posteriorly, while the dorsal tentacular cirri of segments 2 and 3 of *S. brunnea* are long, extending 6–8 segments in length.

Distribution.—Northern California to Baja California in fine, silty sediments, 1263–2955 m.

Sige pleijeli, new species

Fig. 7

Material examined.—California: Santa Maria Basin, off Point Arguello, Sta. 56, 900 m (holotype, USNM 148699).

Description.—A small species, holotype incomplete, broken into 4 parts, totalling 4 mm long and 1 mm wide anteriorly for 43 segments. Body pale, with brown pigment on dorsum and prostomium, dorsal and ventral cirri, and tips of superior presetal lobes.

Prostomium slightly longer than wide, weakly notched on anterior margin, bearing 4 long frontal antennae and 1 shorter, thinner median antennae near anterior end (Fig. 7A); eyes absent. Proboscis appearing smooth in dissection. First segment dorsally reduced, bearing pair of thick tentacular cirri; second segment first with setae, bearing broad dorsal and ventral tentacular cirri; segment 3 with dorsal tentacular cirri and normal ventral cirri (Fig. 7A). Parapodia with podial lobes bearing elongate, finger-

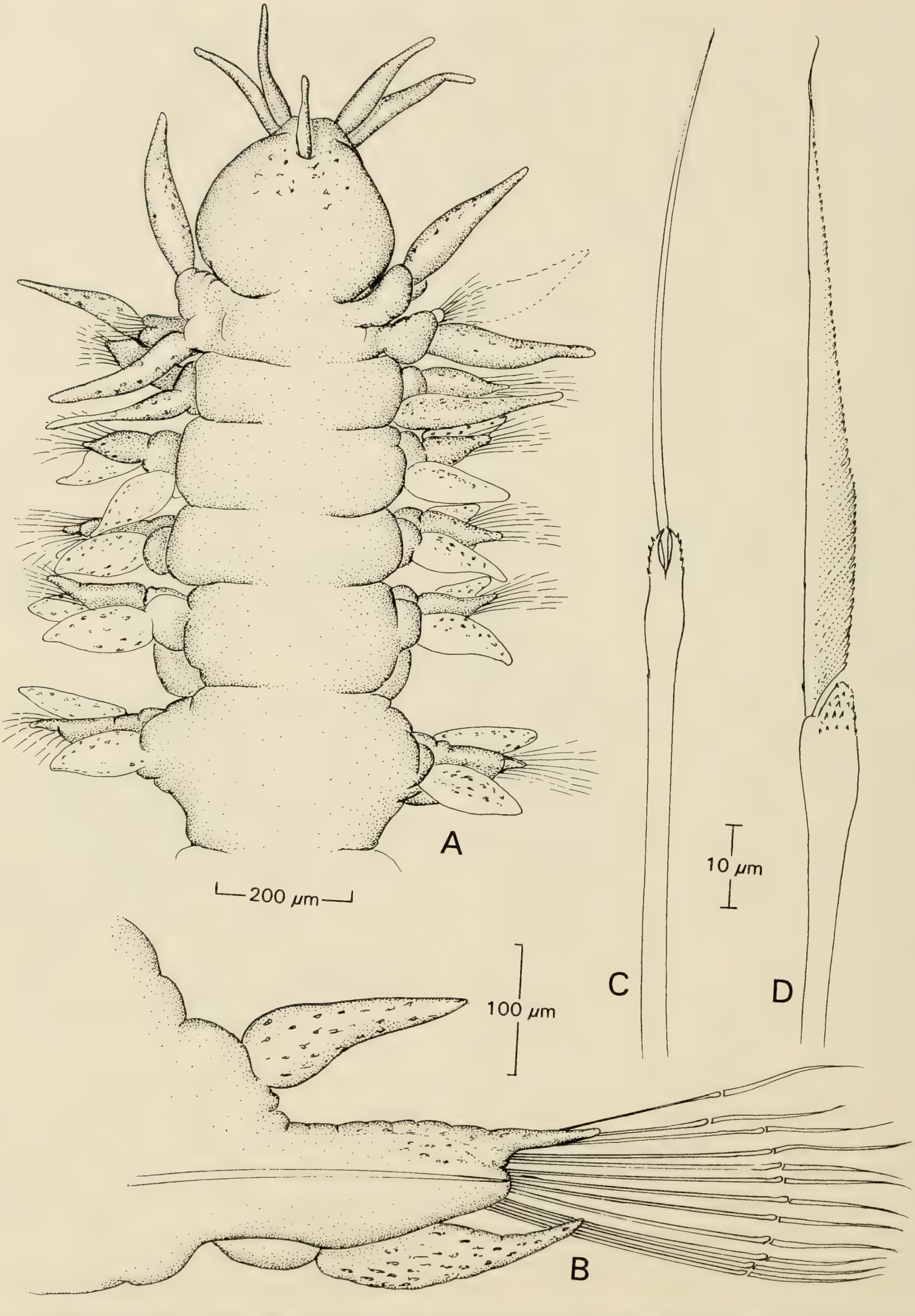

Fig. 7. *Sige pleijeli* (USNM 148699). A, anterior end, dorsal view; B, middle parapodium, posterior view; C–D, setae.

like superior lobe (Fig. 7B); dorsal cirri variable in length along body, usually shorter than ventral cirri, especially in middle and posterior body segments; ventral cirri protruding well beyond tip of inferior podial lobe, but only as long as superior podial lobe (Fig. 7B). Setae numbering 10 to 12 per fascicle, each seta with expanded tip of shaft bearing numerous short teeth on two larger rostral teeth (Fig. 7C); blade with fine denticles along one edge (Fig. 7D). Pygidium unknown.

Remarks.—*Sige pleijeli* differs from all known species of the genus in having the median antenna emerging from the anterior part of the prostomium instead of the center. In this respect the species approaches species of *Pterocirrus,* but is allied to *Sige* in the nature of the elongated superior presetal neuropodial lobe.

The species closely resembles *S. brunnea* (Fauchald, 1972), described from deep-water off Western Mexico to northern California (Fauchald 1972, Pleijel 1990, this study, see above). It differs in the position of the median antenna and in details of the shape of the dorsal and ventral cirri.

Etymology.—This species is named for Dr. Fredrik Pleijel, in recognition of his work on the taxonomy of the Phyllodocidae.

Distribution.—Known only from the upper slope depths off Point Arguello in sediment having 33% sand, 47% silt, and 20% clay; 900 m.

Acknowledgments

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NEW POLYCHAETOUS ANNELIDS OF THE FAMILIES NEREIDIDAE, HESIONIDAE, AND NEPHTYIDAE FROM THE SANTA MARIA BASIN, CALIFORNIA, WITH A REDESCRIPTION OF *GLYCERA NANA* JOHNSON, 1901

Brigitte Hilbig

Abstract.—Four new species of polychaetes belonging to the Nereididae, Hesionidae, and Nephtyidae are described from the Santa Maria Basin off central California, and *Glycera nana* is redescribed based on new material from the same area. The specimens are part of the collections from the California Outer Continental Shelf Monitoring Program that was conducted between 1983 and 1990 for the United States Minerals Management Service. The newly described species are *Nereis ligulata, Gyptis plurisetis, Podarkeopsis perkinsi,* and *Nephtys signifera.*

As part of the California Outer Continental Shelf Monitoring Program performed for the United States Minerals Management Service (MMS) between 1983 and 1990, a rich and highly diverse polychaete fauna was encountered in the Santa Maria Basin in substrata ranging from rocks to fine mud in depths between 50 and 950 m. Although the benthic fauna of California is relatively well known, approximately 25 percent of these polychaete species were found to represent undescribed species. In this paper, four new species are described that belong to the families Nereididae, Hesionidae, and Nephtyidae. Types are deposited at the National Museum of Natural History, Smithsonian Institution (USNM), the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History (LACM-AHF), and the Santa Barbara Museum of Natural History (SBMNH).

Systematic Account

Family Nereididae Johnston, 1845
Genus *Nereis* Linné, 1758

Nereis ligulata, new species
Fig. 1

Nereis nr. *anoculis* Lissner et al., 1986:D-10.

Material examined.—California: Santa Maria Basin, off Port San Luis, Sta. 27, 35°04.30′N, 121°19.27′W, 611 m: holotype (USNM 148701). *Nereis anoculis* Hartman, 1960: holotype (LACM-AHF POLY 000834). *Nereis anoculopsis* Fauchald, 1970: holotype (LACM-AHF POLY 001057).

Description.—Holotype incomplete, in 6 parts; total length 121 mm, width 2.5 mm without parapodia in anterior segments, segments about 190, only last few segments and pygidium absent. Body slender, gradually narrowing toward posterior end behind pharyngeal region, appearing ragged because of elongate parapodia. Color in alcohol uniformly tan; integument wrinkled in anterior segments.

Prostomium longer than wide, roughly hexagonal, with slender, filiform antennae and palps extending anteriorly to about same level, with short conical styles and massive, long palpophores; eyes absent (Fig. 1A).

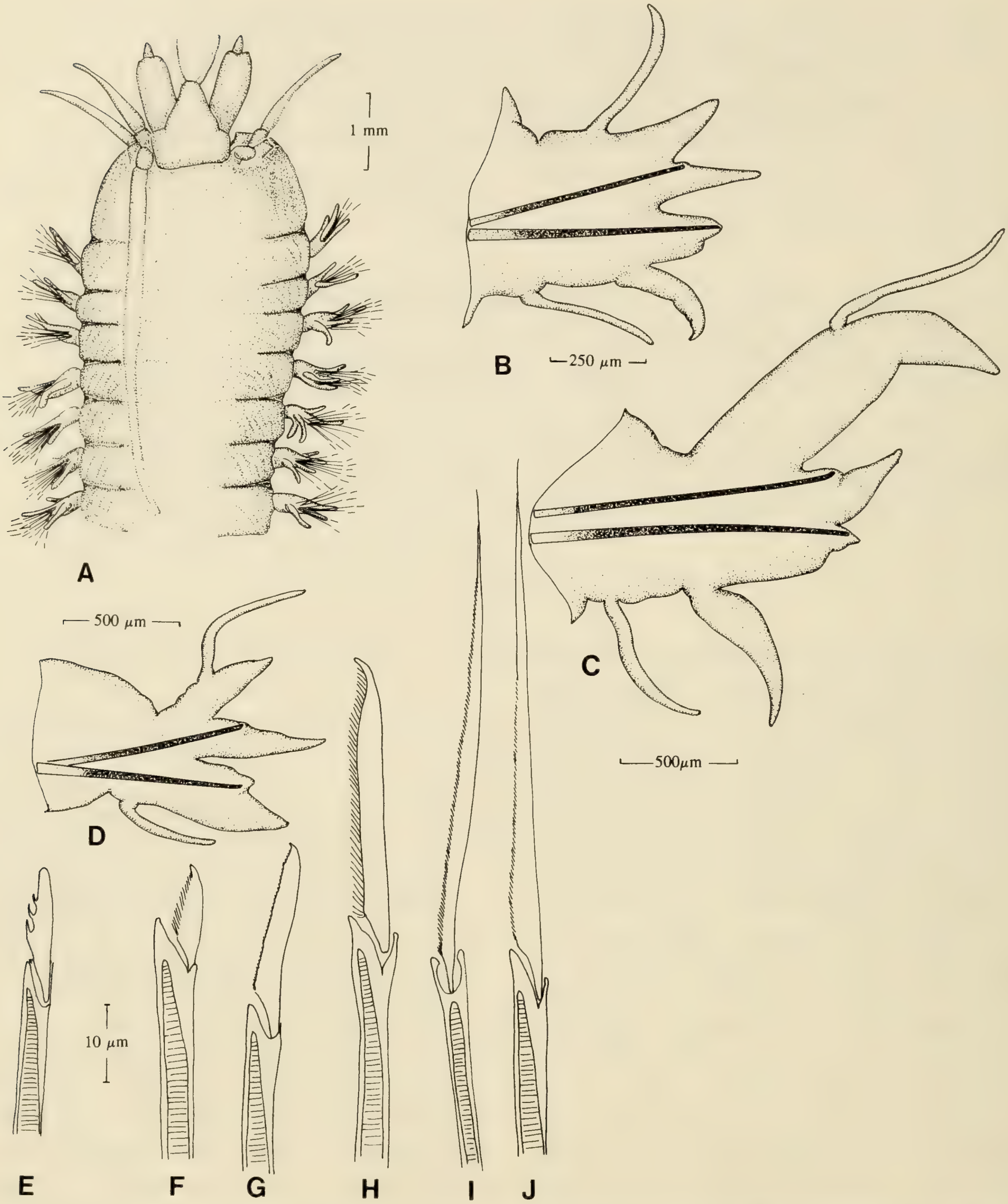

Fig. 1. *Nereis ligulata:* A, anterior end, dorsal view; B–D, anterior, middle, and posterior parapodium, anterior view; E, notopodial homogomph falciger; F, supracicular neuroseta, anterior parapodium; G, same, far posterior parapodium; H, subacicular neuroseta, anterior parapodium; I, neuropodial homogomph spiniger; J, neuropodial heterogomph spiniger (all from holotype).

Proboscis with light brown jaws, each with 15 to 16 pointed teeth; paragnath pattern: Area I: none; II: 5 to 8 in cluster; III: 5 in 1 irregular row; IV: 6 to 7 in arc (largest paragnaths of entire proboscis); V: none; VI: 2 to 3 in row or triangle; VII and VIII: 3 in widely spaced row.

Peristomium about as long as prostomium, 3 times as wide; with 4 pairs tentacular cirri, about as long as peristomium except for second dorsal tentacular cirrus, which reaches back to setiger 6 or 7. Parapodia uniramous in first 2 setigers, biramous thereafter; notopodia with dorsal cirri arising from base of upper ligule in anteriormost segments (Fig. 1B), arising from middle and subdistal positions in mid-body and posterior segments (Fig. 1C–D); upper notopodial ligule pointed, about as long as lower notopodial ligule in first 20 segments (Fig. 1B); in subsequent segments ligule greatly increasing in length (Fig. 1C), with tip becoming glandular. Neuropodia with small acicular lobe and slender, foliaceous lower ligule inserting between ventral cirrus and tip of acicular lobe in anterior and middle setigers, fused to acicular lobe in posterior setigers (Fig. 1D); ventral cirri slender, about as long as dorsal cirri.

Notosetae slender homogomph spinigers from setiger 3 through about 28; homogomph falcigers first appearing in setiger 25, present throughout remaining segments, in posteriormost setigers embedded alongside acicula; blades short, with 3 coarse teeth (Fig. 1E). Upper fascicles of neurosetae with slender homogomph spinigers and, from setiger 16 onward, 1 or 2 heterogomph falcigers; lower fascicles with heterogomph spinigers, from setiger 16 or 17 also with about 5 to 7 heterogomph falcigers; the latter occurring singly in posterior segments and absent in about last 20 segments. All spinigers with finely serrated blades; neuropodial falcigers with blades of varying lengths, in anterior and middle segments with long serrations and distally forming blunt hook; in far posterior segments finely serrated, distally curved and ending in fine point (Fig. 1F–J).

Remarks.—*Nereis ligulata* belongs to a small group of deep-sea species characterized by greatly elongate notopodia with foliaceous upper ligules in posterior segments (Fauchald 1972, Blake 1985, Blake & Hilbig 1990). Within this group, *N. ligulata* most closely resembles *Nereis anoculis* Hartman, 1960, from other deep basins of southern California; the two species differ in the number of teeth on the jaws (7 for *N. anoculis,* 15–16 for *N. ligulata*), the distribution of notopodial spinigers and falcigers (never co-occurring in *N. anoculis,* both present in a few segments in *N. ligulata*), the occurrence of neuropodial falcigers (only in the lower fascicle in *N. anoculis,* both in the upper and lower fascicles in *N. ligulata*), and the number of teeth on the blades of the notopodial falcigers (5 for *N. anoculis,* 3 for *N. ligulata*). Two other species within this group described by Fauchald (1972) from adjacent areas off Mexico, *Nereis angelensis* and *Nereis fossae,* have much greater numbers of paragnaths (38 in areas VII/VIII for *N. angelensis,* 3 for *N. ligulata*; about 20 each in areas III and IV for *N. fossae,* 5–7 for *N. ligulata*). In addition, both *N. fossae* and *N. angelensis* possess eyes, whereas all other species in this group, including *N. ligulata,* are characterized by the absence of eyes. A synopsis of these morphological differences, along with corresponding characteristics of the remaining species belonging to the deep-sea group, is presented in Table 1.

Etymology.—The species name refers to the elongate upper notopodial ligule.

Distribution.—Known only from the type locality, in mixed sand and silt/clay. An additional specimen was found off the Farallon Islands in 995 m depth, but the small size of that individual precluded a definite identification.

Family Hesionidae Sars, 1862

Genus *Gyptis* Marion & Bobretzki, 1875

Diagnosis.—Prostomium with 2 or 3 antennae, median one, if present, attached in central or posterior position; 2 biarticulate palps and usually 2 pairs of lenticular eyes present. Proboscis thin-walled, wide and short when fully extended, with numerous, crowded terminal papillae ("fimbriae" sen-

Table 1.—Morphological features distinguishing deep-sea *Nereis* with elongated upper notopodial ligule (modified after Blake 1985).

Species	Eyes	Jaws No. teeth	Paragnaths								Blades of homogomph falcigers	Reference
			I	II	III	IV	V	VI	VII	VIII		
angelensis	4	0*	2 tandem	11	11 large	12	0	3	{38}		short, smooth	Fauchald 1972
anoculis	0	7	1–3	4 large	4	5–6 large	0	2–3	{4}		5 teeth	Hartman 1960
anoculopsis	0	5–6	2	2	0	4	0	1 small	{2}		short, 5 teeth	Fauchald 1972
fossae	4	7–8	2 tandem	11–13	22	18–20	0	3	{7}		short, smooth	Fauchald 1972
ligulata	0	15–16	0	5–8	5	6–7 large	0	2–3	{3}		3 teeth	This paper
piscesae	0	7–8	2 tandem	ca. 12	21–22	19–20	0	4–6	2 small	4	6–8 blunt teeth	Blake & Hilbig 1990
profundi	0	5	6	14	25	27	2	{few in single row}			long, weakly denticulate	Kirkegaard 1956
sandersi	0	10–12	4–6	ca. 30 small	85–100 in dense field		0	4–5 large	20	1–2 large 3–4 small	short, weakly denticulate	Blake 1985

* Jaws described as "smooth to crenulate."

su Hartman 1968) in up to 4 rows. Eight pairs tentacular cirri arising from 1 or 2 visible segments, smooth to distinctly articulated. Parapodia subbiramous in setiger 1 in some species, biramous from setiger 2 (or 1 in some species). Notosetae numerous, including 1 or more kinds of capillaries and often 1 or 2 acicular spines per fascicle. Neurosetae numerous compound falcigers with long to short blades. Simple setae and shafts of compound setae usually cross-striated.

Remarks.—A generic definition of *Gyptis* is provided here because of considerable confusion in the literature. Hessle (1925) established *Amphidromus,* which was determined by Hartman (1959) to be preoccupied and was renamed *Amphiduros.* One of the diagnostic characters of *Amphiduros* is the smooth anterior margin of the proboscis. However, the generic concept shifted when Hartman (1968) introduced the term "fimbriae" to describe crowded, slender proboscideal papillae which she thought were diagnostic of *Amphiduros. Gyptis* was characterized by 10 or 12 widely spaced, more globular papillae. Perkins (1984) resolved the resulting confusion by transferring a number of species assigned to *Gyptis* (sensu Hartman) to the genus *Podarkeopsis* Laubier, 1961. The genera *Amphiduros, Gyptis,* and *Podarkeopsis* are thus defined as follows: *Amphiduros* includes species with an unpapillated proboscis, as stated originally by Hessle (1925); *Gyptis* includes species with a thin-walled proboscis bearing numerous slender papillae arranged in up to four rows along the anterior margin; and *Podarkeopsis* includes species with a thick, muscular proboscis bearing ten widely spaced papillae.

Gyptis plurisetis, new species

Fig. 2

Hesionidae sp. A Lissner et al., 1986:D-9.—Hyland & Neff, 1988:A-2.—Hyland et al., 1990:F-1.

Amphiduros sp. A Uebelacker, 1984:28–34, figs. 28–30.

Material examined.—California: Santa Maria Basin, Sta. R-1, 35°05.83′N, 120°49.16′W, 91 m: 1 paratype (USNM 148702); Gulf of Mexico, southern Florida, 25°45.70′N, 83°11.07′W, 54 m: holotype (USNM 75314) and 1 paratype (USNM 75315); off Texas, 27°24′N, 96°29′W, 98 m: 1 paratype (USNM 75212).

Description.—Only anterior ends present, length to 2 mm width to 1.3 mm, 5 to 8 setigers. Color in alcohol uniformly tan.

Prostomium oval to pentagonal, distinctly wider than long, with 2 long palps and 3 antennae, the median antenna located just anterior to eyes and about half as long as lateral antennae. Two pairs of large, subequal, round eyes, anterior pair further apart than posterior pair. Nuchal organs developed as crescentic, ciliated grooves along postectal margin of prostomium. Proboscis cylindrical, with numerous deciduous distal papillae (Fig. 2A, B).

Eight pairs of tentacular cirri present on 1 or 2 visible segments, most with styles broken off, remaining ones smooth to indistinctly articulated. Parapodia subbiramous in setiger 1, biramous from setiger 2. Notosetae of four kinds: (1) short, blunt acicular spines, 2 per fascicle (Fig. 2C); (2) long, coarsely serrated capillaries, about as thick as spines, 5 per fascicle; (3) finely serrated capillaries, as long as coarsely serrated ones, but slightly thinner, about 5 per fascicle; and (4) 1 or 2 very thin, smooth capillaries of about same length as spines (Fig. 2D–F). Neurosetae compound falcigers, with long, very delicate, finely serrated blades and smooth shafts. Length/width ratios of blades ranging from 4:1 to 6:1. All notosetae and shafts of neurosetae cross-striated.

Remarks.—*Gyptis plurisetis* was described as *Amphiduros* sp. A by Uebelacker (1984), but is here assigned to the genus *Gyptis* after a reassessment of the generic definitions. *Gyptis plurisetis* resembles most closely *Gyptis vittata* Webster & Benedict, 1887 in the presence of several different types of notosetae (Uebelacker 1984). However, the two species clearly differ in the following characters: lateral antennae and palps are slender and of similar length in *G. plurisetis,* but stout in *G. vittata,* with the antennae clearly longer than the palps; the first papapodia are subbiramous in *G. plurisetis,* but biramous in *G. vittata*; and the notosetae include smooth spines and three types of capillary setae in *G. plurisetis,* but two kinds of serrated spines, fine-tipped serrated setae, and serrated capillary setae in *G. vittata.* In addition, the proboscis of *G. plurisetis* bears numerous slender papillae, whereas *G. vittata* has a proboscis with 10 papillae and may belong to *Podarkeopsis* although forked notosetae are absent.

Habitat.—The species occurs in low densities in silty clay and coarse to fine sands.

Etymology.—The species name is derived from *plus* (Latin for many), and seta to reflect the numerous types of notosetae.

Distribution.—Gulf of Mexico: Florida to Texas; central California; 40 to 100 m.

Genus *Podarkeopsis* Laubier, 1961

Diagnosis.—Prostomium with 3 antennae, with median one attached in frontal position; with 2 biarticulate palps and 2 pairs of lenticular eyes. Proboscis cylindrical, with thick muscular layer and 10 terminal papillae that may alternate with tufts of cilia. Eight pairs tentacular cirri arising from 3 visible segments, smooth to distinctly articulated. Parapodia subbiramous in setigers 1 to maximally 4, biramous thereafter. Notosetae few, including furcate setae, acicular spines and occasionally some capillaries, smooth or serrated, with or without cross-striations. Neurosetae numerous compound falcigers.

Remarks.—This genus was established by Laubier (1961) to accommodate a species that resembles *Podarke* in having furcate notosetae, but possesses eight rather than six pairs of tentacular cirri. In subsequent years, the presence of furcate setae was not considered a generic level character, but rather a species character, and the status of

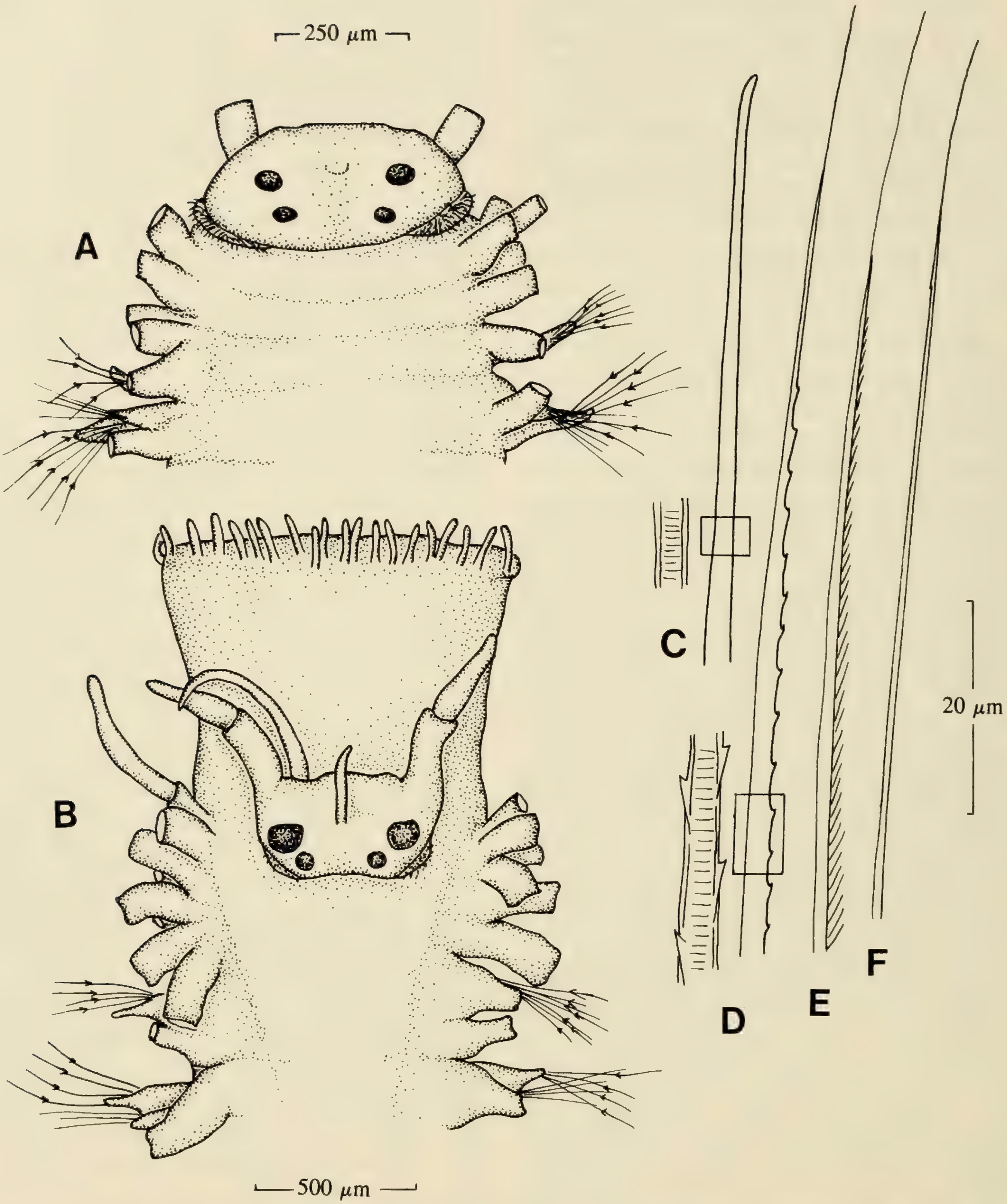

Fig. 2. *Gyptis plurisetis:* A, anterior end, dorsal view; B, same, specimen from the Gulf of Mexico (after Uebelacker 1984); C, notopodial spine with detail of cross-striation; D, coarsely serrated capillary with detail of cross-striation and serrations; E, finely serrated capillary; F, smooth capillary (A, C–F from paratype USNM 148702).

Podarkeopsis was unclear. Perkins (1984), however, reestablished the genus and referred a number of *Gyptis* species with furcate setae to *Podarkeopsis*. The genus now includes a well-defined group of species with eight pairs of tentacular cirri. *Podarkeopsis brevipalpa,* formerly a "catch-all species" for specimens with furcate notosetae and 8

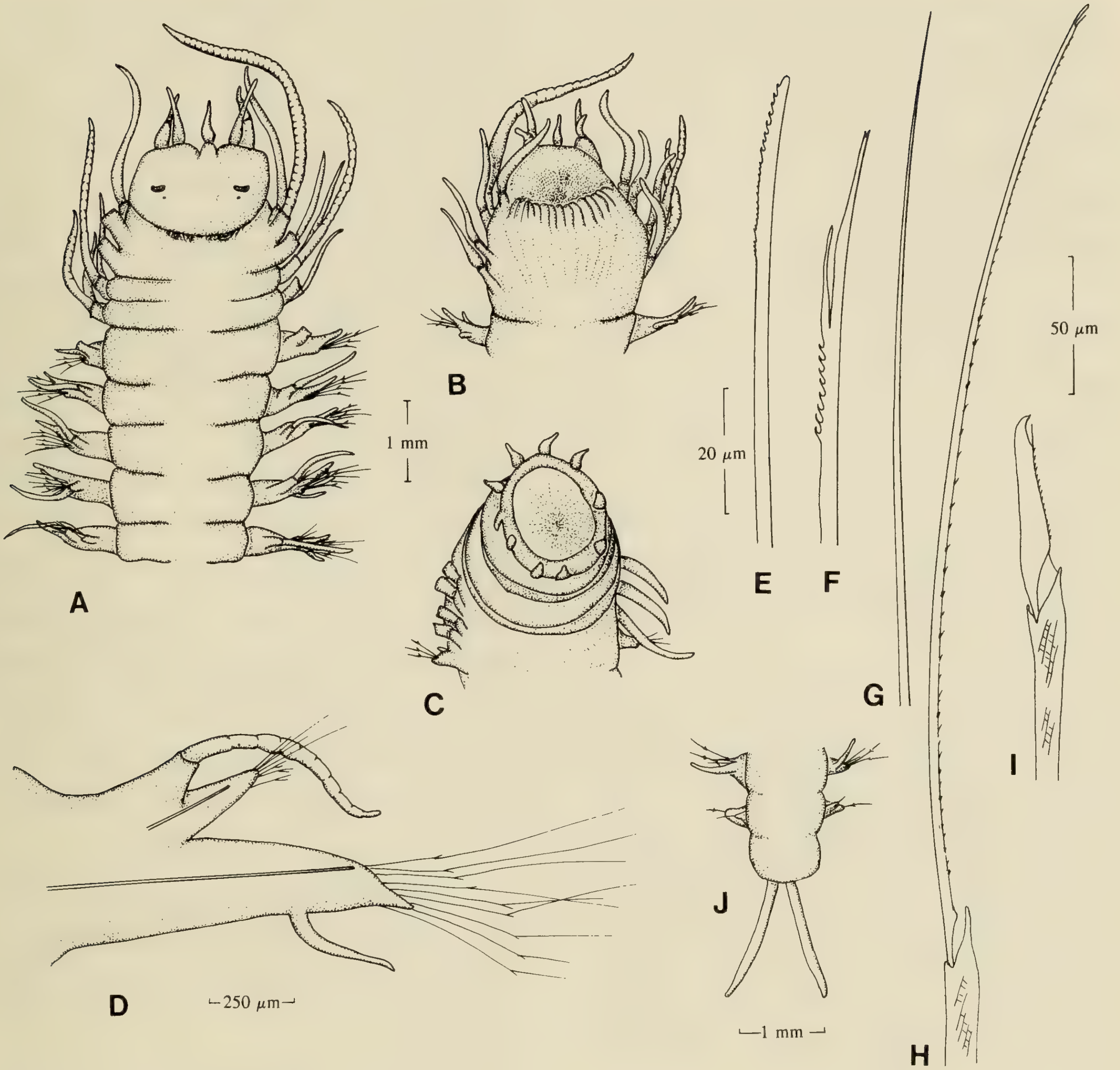

Fig. 3. *Podarkeopsis perkinsi:* A, anterior end, dorsal view; B, same, ventral view; C, proboscis, anteroventral view; D, parapodium; E, notopodial spine; F, furcate notoseta; G, capillary notoseta; H, long-bladed neuroseta; I, short-bladed neuroseta; J, posterior end, dorsal view (all from paratype USNM 148705).

pairs of tentacular cirri (as *Gyptis brevipalpa*) appears to be restricted to intertidal and shallow subtidal depths and was not found in the California material available to this author, but may co-occur with the relatively common *Podarkeopsis glabra* (Hartman, 1961). *Podarkeopsis brevipalpa* was originally described from El Salvador (Hartmann-Schröder 1959) and has been reported from Oregon and Washington (confirmed by the author).

Podarkeopsis perkinsi, new species
Fig. 3

Podarkeopsis sp. A Lissner et al., 1986: D-9.

Podarkeopsis sp. B Lissner et al., 1986:D-9.—Hyland & Neff, 1988:A-2.—Hyland et al., 1990:F-1.

Material examined.—California: Santa Maria Basin, Sta. R-6, 34°41.40′N, 120°57.90′W, 410 m: holotype (USNM

148703), Sta. 26, 35°04.38'N, 121°15.99'W, 590 m: 1 paratype (USNM 148704), Sta. 28, 35°04.22'N, 121°19.65'W, 603 m: 1 paratype (USNM 148705), Sta. 61, 34°33.01'N, 120°48.89'W, 345 m: 1 paratype (LACM-AHF POLY 1617), Sta. 76, 34°25.59'N, 120°40.98'W, 387 m: 1 paratype (LACM-AHF POLY 1618), Sta. R-3, 35°05.30'N, 121°00.90'W, 409 m: 2 paratypes (SBMNH 35619), Sta. R-9, 34°53.68'N, 120°59.12'W, 410 m: 1 paratype (SBMNH 35620). Off Farallon Islands, Sta. 3-3, 37°27.25'N, 123°07.66'W, 800 m (1), Sta. 4-7, 37°13.47'N, 123°07.48'W, 1020 m (1).

Description.—Length to 18 mm, width to 2 mm, segments to 51. Body slender, widest in pharyngeal region, gradually tapering toward pygidium. Color in alcohol uniformly tan.

Prostomium pentagonal, with 3 antennae, 2 palps, and 2 pairs of eyes (occasionally faded in alcohol), anterior pair as far apart as posterior pair, moderately large, kidney-shaped; posterior pair minute rounded spots. Lateral antennae about as long as palps, median antenna about half as long; palps directed toward ventrum. Two heavily ciliated nuchal organs along postectal margins of prostomium (Fig. 3A). Proboscis with 10 large terminal papillae (Fig. 3C) and ciliary band.

Eight pairs of tentacular cirri on 3 visible segments; first 4 pairs on segment 1, dorsal cirri of first pair longest, all ventral tentacular cirri considerably shorter than corresponding dorsal ones (Fig. 3A, B). Parapodia subbiramous in setigers 1 to 3, biramous thereafter; notopodia about half as long as neuropodia, with conical presetal lobe; dorsal cirri extending to tip of neuropodium, indistinctly articulated or wrinkled, attached to wide cirrophore. Neuropodia with long, conical presetal lobe; ventral cirri short, slender, smooth, inserted subdistally (Fig. 3D).

Notosetae first present in setiger 4; including up to 6 furcate setae in dorsalmost position, up to 14 finely serrated, very slender capillaries in middle position, and up to 6 distally coarsely serrated spines in ventralmost position; ventralmost setae in juveniles appearing as cultriform setae with flattened and serrated tip (Fig. 3E–G). Neurosetae compound, arranged in two groups: dorsal fascicle of numerous, very long-bladed and slender falcigers and ventral fascicle of few short-bladed falcigers (Fig. 3H, I).

Pygidium small, surrounding terminal anus, with 2 slender ventrally inserted anal cirri (Fig. 3J).

Remarks.—*Podarkeopsis perkinsi* is easily recognized by the occurrence of the first notopodia in setiger 4 (rather than 5 as is typical for the genus) and the setal morphology. The serrations on the notopodial spines and the extremely long-bladed upper neurosetae are diagnostic for this species. *Podarkeopsis perkinsi* differs from *P. glabra* most obviously by the presence of capillary setae in the notopodial fascicle and the occurrence of notosetae from setiger 4 rather than 5.

Habitat.—The species is found in silt and sand on the upper and middle slope.

Etymology.—This species is named after Tom Perkins in recognition of his valuable contributions to the systematics of the Hesionidae.

Distribution.—Known only from off central California, 385 to 1020 m.

Family Glyceridae Grube, 1850
Genus *Glycera* Savigny, 1818
Glycera nana Johnson, 1901
Fig. 4

Glycera nana Johnson, 1901:411, pl. 10, figs. 103, 103a.

Glycera capitata Hartman, 1950:76, pl. 11, figs. 1–4 (in part); 1968:617 (in part).—Hyland & Neff, 1988:A-2.—Hyland et al., 1990:F-1.—*Not* Oersted, 1843.

Material examined.–Holotype: Puget Sound (MZC 1878). California: Santa Maria Basin, Sta. PJ-1, 34°55.79'N,

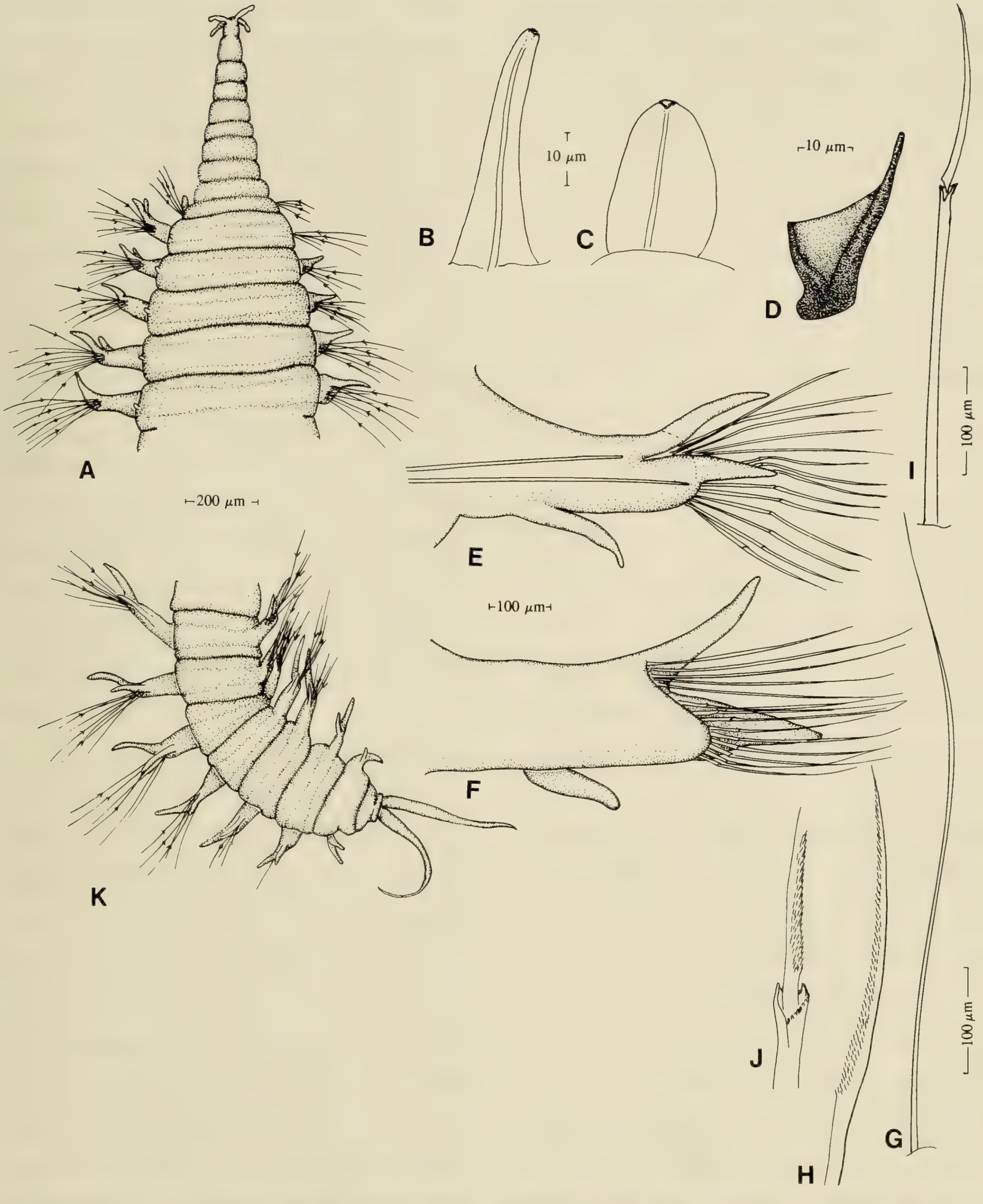

Fig. 4. *Glycera nana:* A, anterior end, dorsal view; B–C, proboscideal organs; D, aileron; E, middle parapodium, anterior view; F, same, posterior view; G, notoseta; H, tip of notoseta; I, neuroseta; J, insertion of blade; K, posterior end, ventral view (all from Californian specimens).

120°49.91′W, 145 m (3); Sta. PJ-2, 34°55.32′N, 120°49.59′W, 142 m (9); Sta. PJ-3, 34°56.26′N, 120°49.58′W, 138 m (1); Sta. PJ-4, 34°56.26′N, 120°50.24′W, 150 m (2); Sta. PJ-5, 34°55.32′N, 120°50.24′W, 152 m (7); Sta. PJ-6, 34°54.71′N, 120°49.91′W, 148 m (3); Sta. PJ-7, 34°55.79′N, 120°48.60′W, 123 m (6); Sta. PJ-8, 34°56.87′N, 120°49.91′W, 142 m (9); Sta. PJ-10, 34°53.65′N, 120°49.91′W, 147 m (5). Off the Farallon Islands, Sta. 4-7, 37°13.47′N, 123°07.48′W, 1020 m (5); Sta. 4-14, 37°14.75′N, 123°05.82′W, 812 m (2).

Description.—Length to 64 mm, width excluding parapodia to 4 mm, segments at least 140. Holotype 30 mm long, 3 mm wide (excluding parapodia) for 69 setigers; largest specimen from California 25 mm long, 2 mm wide for 107 setigers. Body of holotype robust, of California specimens slender, tapering at both ends, widest in pharyngeal region. Segments distinctly triannulate throughout, short and crowded in anterior half of body (Fig. 4A), somewhat longer in posterior half; with long, slender parapodia. Color in alcohol: tan, sometimes with scattered dark pigmentation on tips of parapodial lobes in posterior segments; dorsal body wall sometimes rugose and slightly darkened in anterior segments of mature specimens.

Prostomium pointed, much longer than wide, with 8 to 10 rings; basal annulus much narrower than peristomium in holotype, only slightly narrower than peristomium in Californian specimens (Fig. 4A). Proboscis densely covered with proboscideal organs of two kinds: most numerous ones tall, slender, at least three times as long as basal width, with terminal pore and smooth surface; second type oval, less than twice as tall as basal width, flat in side view, smooth, scattered among tall ones (Fig. 4B, C). Ailerons with moderately long outer ramus and short inner ramus completely fused to interramal plate (Fig. 4D). Peristomium with two dorsolateral nuchal slits.

Parapodia conspicuous, reaching about one-half body width in pharyngeal region and surpassing body width in posterior segments of smaller specimens; with two slender, pointed, subequal presetal lobes and single, rounded, much shorter postsetal lobe; dorsal cirri small, papilliform, ventral cirri slender, conial, about as long as dorsal presetal lobe (Fig. 4E, F). Setae long, flowing; notosetae simple capillaries, finely serrated in upper third (Fig. 4G, H); neurosetae compound spinigers, twice as wide as notosetae, with finely serrated blades (Fig. 4I, J).

Posterior end slender, tapering to small, ring-shaped pygidium bearing two slender anal cirri (Fig. 4K).

Remarks.—As part of a recent revision of North Atlantic glycerids, O'Connor (1986) noted that *Glycera capitata* had become a "catch-all" species for forms with single, rounded postsetal lobes and smooth proboscideal organs. He identified at least five different species with these characters and emphasized the taxonomic importance of characters such as the aileron and the number of annuli per segment. The result is a much more precise definition of *G. capitata,* with the consequence that several of the North American specimens assigned to *G. capitata* no longer agree with the species description, including the Californian specimens described here that were originally identified as *G. capitata* (Hyland & Neff 1988, Hyland et al. 1990).

Johnson (1901) described *Glycera nana* as possessing biannulate segments and parapodia with short presetal lobes and ventral cirri, and initially the California specimens described here were thought to belong to an undescribed species because of their triannulate segments and relatively long, conical presetal lobes and ventral cirri. However, the holotype of *G. nana* was found to have triannulate segments and parapodia with long presetal lobes and ventral cirri. Johnson's (1901) description and illustrations are therefore either incorrect, or he treated a mixture of two species, possibly *G. nana* and *G. capitata.* Both species have been seen by the author in several collections from the Puget Sound (Washington) and Kodiak and Prince William Sound (Alaska). Hartman (1950) based her synonymy of those two species on the proportions of parapodial lobes and cirri without considering the number of segmental annuli, but stated that her "northern form" of *G. capitata,* characterized by very short presetal lobes and ventral cirri, should be assigned to *G. nana* should that name prove to remain valid. Her "southern form," characterized by long presetal lobes and ventral cirri, would then represent the Pacific populations of *G. capitata.* The examination of the holotype of *G. nana,* however, suggests that Hartman's "northern form" belongs to *G. capitata,* whereas the "southern form" belongs to *G. nana.*

Another co-occurring species of *Glycera* with only one postsetal lobe, *Glycera branchiopoda* Moore, 1911, is easily distinguished from *G. nana* by the foliaceous, rather than conical, ventral cirri that distinctly extend beyond the postsetal lobe.

Distribution.—Off central California, 123–1020 m, in mixed sand and silt.

Family Nephtyidae Grube, 1850

Genus *Nephtys* Cuvier, 1817

Nephtys signifera, new species

Fig. 5

Nephtys sp. A Lissner et al., 1986:D-10.
Nephtys sp. H. Hyland & Neff, 1988:A-2.

Material examined.—California: Santa Maria Basin, Sta. R-2, 35°05.50′N, 120°49.16′W, 161 m: holotype (USNM 148706) and 1 paratype (USNM 148707), Sta. 13, 35°14.54′N, 120°59.77′W, 197 m: 3 paratypes (SBMNH 35617), Sta. 30, 34°54.19′N, 120°47.07′W, 98 m: 6 paratypes (SBMNH 35618), Sta. PJ-1, 34°55.79′N, 120°49.91′W, 145 m: 1 paratype (LACM-AHF POLY 1615), Sta. PJ-6, 34°54.71′N, 120°49.91′W, 148 m: 1 paratype (LACM-AHF POLY 1616).

Description.—Length to 28 mm, width to 2 mm excluding parapodia, segments to 77. Body unpigmented except for central red eyespot on prostomium and dark brown to black subdermal eyes on setiger 3 in juveniles; setae dusky.

Prostomium quadrangular, about as long as wide when proboscis is retracted; oval and wider than long when proboscis is everted. Dorsal antennae smallest and well separated from ventral ones (Fig. 5A, B). Dorsolateral edges below ventral antennae staining distinctly in methyl green (Fig. 5B); staining often including outer edges of brain and ventral edge of mouth. Proboscis proximally smooth, with 22 rows of about 5 papillae and a single middorsal papilla; distally surrounded with 20 bifid papillae (Fig. 5C).

First parapodia directed forward, reduced, with large ventral cirri and very long setae projecting well beyond prostomium. Subsequent parapodia in anterior part of body with low, rounded presetal lamellae, deeply incised acicular lobes, and bluntly rounded postacicular lamellae; notopodial postacicular lamellae pointed toward middorsum, neuropodial ones pointed slightly upward. Parapodia of middle and posterior segments similar to anterior parapodia except for slight changes in proportion (Fig. 5D); incision of acicular lobes becoming progressively shallower, acicular lobes turning conical, and postacicular lamellae gradually diminishing in size and reduced in posterior segments. Interramal cirri first present on segment 3, small at first; wide, flattened, straight, (occasionally slightly curved), in posterior segments more slender; heavily ciliated; occupying about one-third to one-half of interramal space. Dorsal cirri small and slender throughout; ventral cirri larger, conical.

Aciculae with curved, dusky tips. Preacicular setae crossbarred, short and stiff (Fig. 5E); postacicular setae of both rami smooth to spinulose and slender in small uppermost and lowermost fascicles, basally spinose in middle fascicles (Fig. 5F, G).

Pygidium with filiform anal cirrus.

Remarks.—*Nephtys signifera* belongs to a small group of closely related, co-occurring species characterized by interramal cirri that start on segment 3 and are in most cases straight and relatively short throughout. This group includes *Nephtys californiensis* Hartman, 1938, *Nephtys ferruginea*

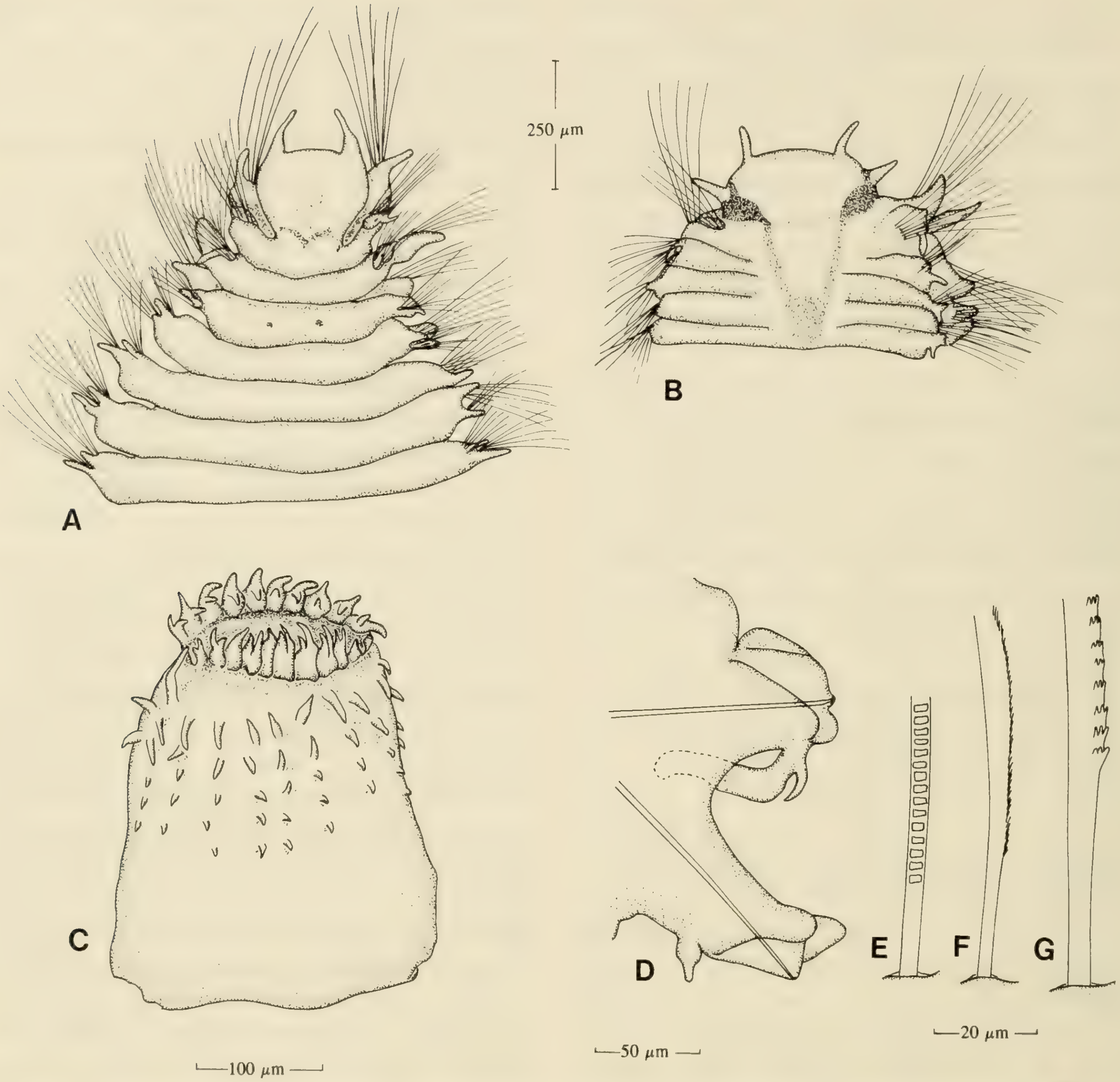

Fig. 5. *Nephtys signifera:* A, anterior end, dorsal view; B, same, showing methyl green staining pattern; C, proboscis, lateral view; D, middle parapodium, anterior view; E, preacicular seta; F, spinulose postacicular seta; G, spinose postacicular seta (A from additional specimen; B, E–G from paratype LACM-AHF POLY 1615; C, D from paratype LACM-AHF POLY 1616).

Hartman, 1940, *Nephtys magellanica* Augener, 1912, and *Nephtys simoni* Perkins, 1980. *Nephtys signifera* differs from these species most conspicuously by the presence of a glandular area along the dorsolateral edges of the prostomium that stains with methyl green. Additionally, all the above mentioned species (with the exception of *N. magellanica*) have 22 rather than 20 distal papillae on the proboscis, and the distribution of spinose, spinulose, and smooth setae in the postacicular fascicle is distinctly different from that found in *N. signifera*. *N. ferruginea* has spinulose setae in the upper notopodial and lower neuropodial fascicles and spinose setae in the lower notopodial and upper neuropodial fascicles; *N. magellanica* has smooth setae in the upper noto- and neuropodial fascicles, spinose setae in the middle noto- and neuropodial fascicles, and spinulose setae in the lower noto- and neuropodial fascicles; and *N. simoni* has smooth setae in the lower notopodial and upper neuropodial fascicles and basally spinose setae in the upper notopodial and lower neuropodial fascicles. The postacicular setae of *N. californiensis* are similar to those of *N. signifera* (smooth to spinulose in upper and lower noto- and neuropodial fascicles, spinose in middle noto- and neuropodial fascicles), but the two species differ in the presence of a middorsal proboscideal papilla. *N. magellanica* resembles *N. signifera* most closely; it differs from *N. signifera* in the number of subdistal rows of proboscideal papillae (20 rather than 22). It is possible that some of the specimens that Hartman (1950) assigned to *N. californiensis,* even though they had a middorsal proboscideal papilla, belong to *N. signifera.*

Habitat.—The species is found in sediments with high contents of sand or about equal amounts of sand and silt.

Etymology.—The species name is derived from *signum* (Latin for mark) and *fere* (Latin for to bear) and refers to the distinct and unusual methyl green staining pattern.

Distribution.—Known only from central California, 110–220 m.

Acknowledgments

I am grateful to James A. Blake and R. Eugene Ruff for many helpful discussions and a careful review of a draft of this paper, and to Brendan O'Connor for examining some specimens of *Glycera nana.* Howard R. Jones was the first to discover the unusual methyl green staining pattern of *Nephtys signifera.* The National Museum of Natural History, Smithsonian Institution, kindly provided the voucher specimens of *Amphiduros* sp. A. Types and additional specimens of *Nephtys ferruginea, Nephtys magellanica, Nephtys simoni, Nereis anoculis,* and *Nereis anoculopsis* were provided by the Los Angeles County Museum of Natural History. I would like to thank the Museum of Comparative Zoology, Harvard, for generous assistance with the redescription of *Glycera nana,* and Chris Glasby for his kind and helpful comments especially on the hesionids treated in this paper. The manuscript also benefitted from the comments of an anonymous reviewer. This study was funded by the Pacific Outer Continental Shelf Region of the Minerals Management Service, U.S. Department of the Interior, Washington, D.C., under Contract No. 14-35-0001-30484.

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POLYCHAETA FROM DEEP-SEA HYDROTHERMAL VENTS IN THE EASTERN PACIFIC. III. A NEW GENUS AND TWO NEW SPECIES OF SPIONIDAE FROM THE GUAYMAS BASIN AND JUAN DE FUCA RIDGE WITH COMMENTS ON A RELATED SPECIES FROM THE WESTERN NORTH ATLANTIC

James A. Blake and Nancy J. Maciolek

Abstract.—Two new species of Spionidae were found in soft sediments at the Guaymas Basin and Juan de Fuca Ridge hydrothermal vent fields. These new spionids are unusual in having modified notopodial spines in anterior setigers and for possessing ventral as well as dorsal branchiae. Ventral branchiae have not been previously reported for the family. The presence of modified neuropodial spines in anterior setigers allies these species with the shallow water genus *Scolecolepides,* however, a new genus, *Lindaspio,* is established because branchiae begin on setiger 2 instead of 1. The two new species, *L. dibranchiata* and *L. southwardorum,* are large, with the latter species from the Juan de Fuca Ridge, being one of the largest spionids ever reported. A previously described species, *S. caruncultatus,* from ambient sediments on the continental slope off North Carolina has been reexamined and referred to the new genus *Lindaspio.* All three species are described and compared.

Approximately 63 polychaete species have been reported as occurring in the vicinity of active hydrothermal vents in the eastern Pacific (summarized by Blake & Hilbig 1990). At least another 25–30 species remain to be described from material already collected.

Three species of Spionidae including two genera, *Lauberiellus* and *Xandaros,* were described from the Galapagos Rift hydrothermal vents by Maciolek (1981). *Xandaros* appears to be restricted to vent habitats. The third species, *Prionospio sandersi,* was associated with the vestimentiferan *Riftia pachyptila.* No additional spionids have been described from vent ecosystems, although Blake & Hilbig (1990) reported a single specimen of an unidentified species of *Prionospio* from the Juan de Fuca Ridge. Recent expeditions to hydrothermal vent areas in the Guaymas Basin and Gorda Ridge by J. F. Grassle, and the Juan de Fuca Ridge by Verena Tunnicliffe and her associates have yielded additional spionids.

The present paper describes a new genus of Spionidae that was first collected by J. F. Grassle from sediments associated with hydrothermal mounds in the Guaymas Basin. This new spionid is unusual in possessing anterior notopodial spines and ventral branchiae. A second species was collected by Eve Southward, Alan J. Southward, and Verena Tunnicliffe from sediments near hydrothermal vents on the Juan de Fuca Ridge. These two species are referred to a new genus, *Lindaspio,* that has branchiae from setiger 2 and modified anterior neurosetae. A continental slope species from off North Carolina, *Scolecolepides carunculatus*

tus Maciolek, has been reexamined and is also referred to this new genus.

The collections are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.

Systematic Account

Family Spionidae

Lindaspio, new genus

Type species.—*Lindaspio dibranchiata,* new species. Gender feminine.

Diagnosis.—Prostomium incised, developed into 2 frontal lobes or weak horns; caruncle short; occipital tentacle lacking. Peristomium lacking lateral wings. Dorsal branchiae from setiger 2, ventral branchiae from an anterior segment, or ventral branchiae completely absent; branchiae closely associated with parapodial lamellae, continuing to posterior end. Setiger 1 reduced, with notopodia reduced to single lamella lacking notosetae; notopodia and neuropodia with capillaries and hooded hooks; some anterior notopodia with rosettes or clusters of heavy pointed spines, or spines absent; anterior neuropodia with fascicles of heavy spines. Genital pouches lacking. Pygidium simple, conical, lacking cirri.

Etymology.—The genus, *Lindaspio,* is named in memory of Linda Morse-Porteous, deep-sea biologist of the Woods Hole Oceanographic Institution, a colleague and friend who left us too soon.

Remarks.—*Lindaspio* is closely related to species belonging to the nearshore genus, *Scolecolepides* as revised by Maciolek (1984). Both genera have anterior setigers with modified neuropodial spines and anteriorly bifurcated prostomia, sometimes expanded into frontal horns. *Lindaspio,* however, has branchiae beginning from setiger 2 instead of setiger 1. Further, the three species assigned to *Lindaspio* are from deep-sea habitats, where species of *Scolecolepides* are only known from nearshore estuarine habitats.

Three species are assigned to this genus:

Lindaspio dibranchiata, new species
L. southwardorum, new species
L. caruncluata (Maciolek, 1984),
new combination

Lindaspio dibranchiata, new species
Figs. 1, 2

Material examined.—Guaymas Basin, Southern Trough, hydrothermal mounds, *Alvin* Dive 1606, box core No. 1, 28 Jul 1985, 27°01′N, 111°24′W, 2008 m, paratype (USNM 148672); *Alvin* Dive 1614, box core No. 3, 6 Aug 1985, 27°01′N, 111°24′W, 2004 m, holotype (USNM 148673).

Description.—Holotype complete, 31 mm long and 4 mm wide for about 165 crowded setigers; small paratype incomplete anterior fragment 2.6 mm long and 1.0 mm wide for 22 setigers. Color in alcohol: brown. Anterior end broad, widest between setigers 12–20, dorsoventrally flattened throughout. Body terminating in conical pygidial cone, lacking appendages.

Prostomium bifid anteriorly, formed into two thick rounded lobes or horns, extending posteriorly as short, mounded caruncle, terminating indistinctly at end of first setiger (Fig. 1A). Palps short, thick. Setiger 1 reduced, lacking notosetae, notopodium reduced to single flattened lamella; neuropodium with well-developed pre- and postsetal lamellae and fascicles of capillaries; following segments with well-developed noto- and neuropodia bearing elaborate pre- and postsetal lamellae encompassing setal fascicles (Fig. 1A). Notopodia of middle and posterior setigers with anterior and posterior lamellae, but these lamellae shorter, more triangular and only partly encompassing setae.

Dorsal branchiae present from setiger 2, closely adhering to base of postsetal lamellae (Figs. 1A, 2A); each anterior branchia thickened, extending across dorsal midline; after setiger 20, dorsal branchiae becoming thin, continuing to posterior end. Ventral

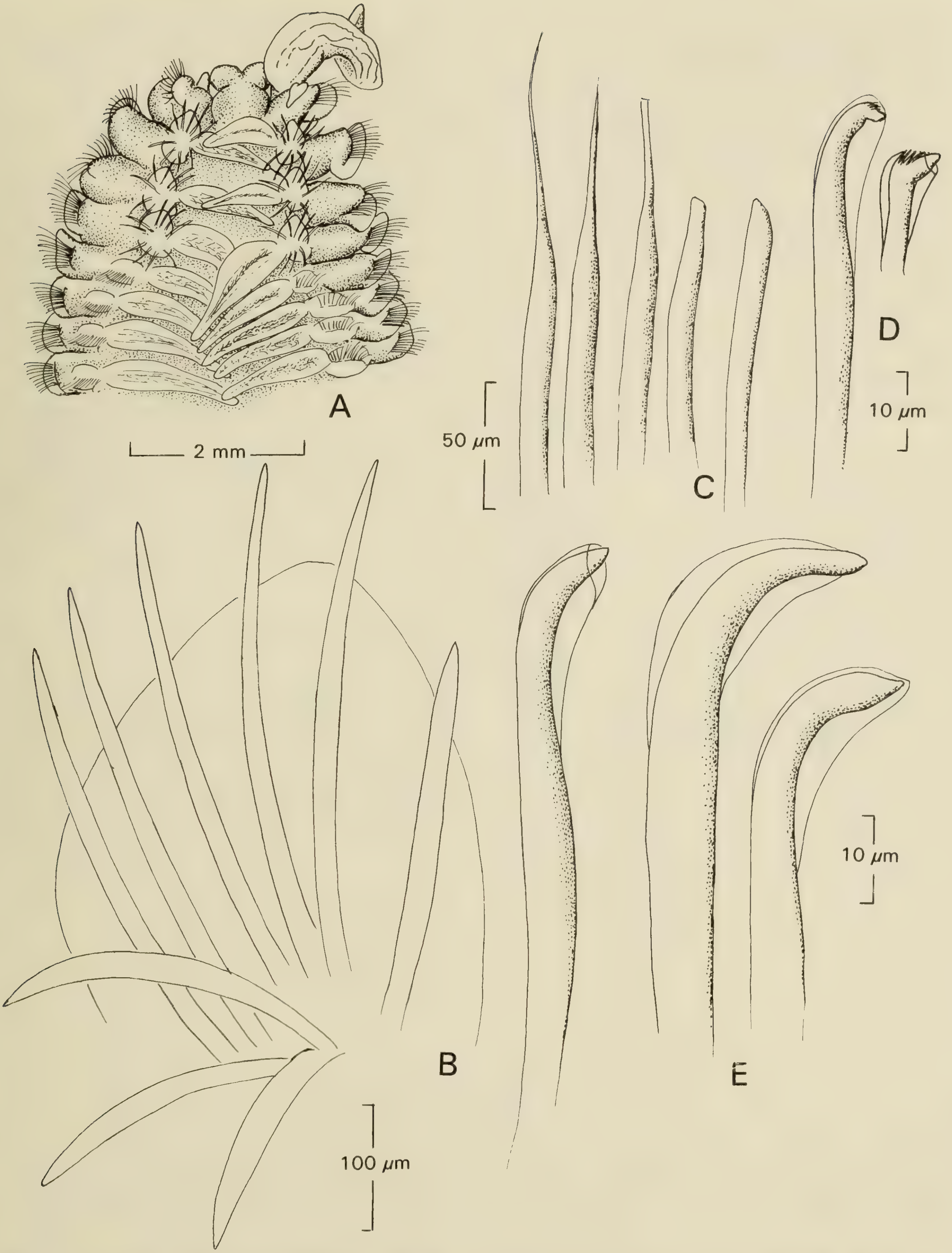

Fig. 1. *Lindaspio dibranchiata* (USNM 148673). A, Anterior end, dorsal view; B, Fascicle of modified notopodial spines from anterior setiger; C, Modified neuropodial spines, unworn and worn; D, Neuropodial hooded hooks; E, Notopodial hooded hooks.

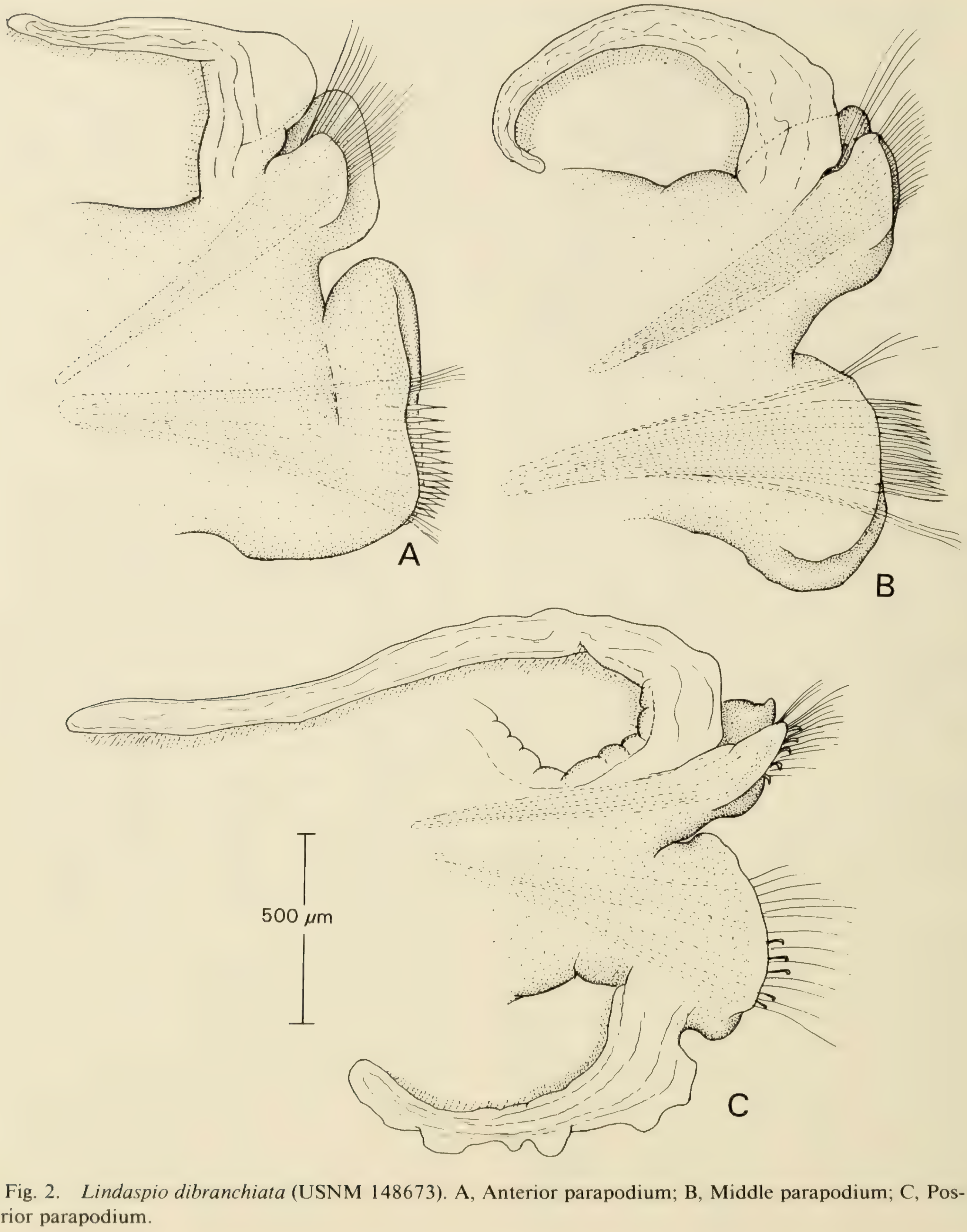

Fig. 2. *Lindaspio dibranchiata* (USNM 148673). A, Anterior parapodium; B, Middle parapodium; C, Posterior parapodium.

branchiae first apparent from about setiger 20 as swollen protuberance of neuropodium (Fig. 2B), becoming well developed by setiger 30 and fully developed by setiger 40 (Fig. 2C); ventral branchiae broader than dorsal branchiae, not meeting at ventral midline, continuing to posterior end.

Notosetae of setigers 2–4 modified into rosettes of 9–10 heavy spines (Fig. 1A, B); subsequent notosetae consisting of capillaries until about setiger 40 where 3–5 unidentate hooded hooks begin; hooks sharply curved with closely adhering hood (Fig. 1E). Neurosetae of setigers 1–5 all capillaries; with distinct fascicles of 15–20 heavy spines and thin capillaries from setigers 6–28 (Figs. 1C, 2A, B); spines replaced by multidentate hooded hooks by about setiger 45 (Figs. 1D, 2C); neuropodial spines distinctly tapered distally (Fig. 1C), when worn, appearing acicular; neuropodial hooks thinner, more delicate than notopodial hooks (paratype).

Remarks.—See comments under *Lindaspio southwardorum* (below).

Etymology.—The specific name is derived from the Greek, *di* for two or double, and *branchos,* for gill, referring to presence of both dorsal and ventral branchiae that occur on this species.

Lindaspio southwardorum, new species
Fig. 3

Material examined.—Juan de Fuca Ridge, Middle Valley Segment, *Alvin* Dive 2252-3324, 6 Aug 1990, 48°25.8′N, 128°40.9′W, 2425 m, from box core in high-heat-flow area, holotype (USNM 148674); same location and dive, Collection No. A2252-3327, large fragments (JAB).

Description.—A large species, holotype broken into several fragments totaling 341 setigerous segments, 159 mm long, and 6–7 mm wide; anterior fragment with 57 setigerous segments; second, anteriorly incomplete specimen, larger, in two sections, 110 mm long, 8 mm wide. Color in life: pinkish white with pale violet streak down dorsum; color in alcohol: light brown. Anterior half of body dorsoventrally flattened, with dorsum becoming rounded posteriorly. Pygidium not present among fragments.

Prostomium narrow, pear-shaped, flaring anteriorly, forming two broadly swollen lobes, continuing posteriorly as narrow, folded caruncle to anterior margin of setiger 2 (Fig. 3A). Palps short, thick. Setiger 1 reduced, lacking notosetae, neuropodium with well-developed pre- and postsetal lamellae and fascicles of capillaries, notopodium reduced to flattened lamella. Notopodia of setigers 2–4 modified, dorsally elevated, with pre- and postsetal lamellae forming cup enclosing cluster of modified spines (Fig. 3A); notopodia from setiger 5 and neuropodia from setiger 2 with well-developed, elaborate pre- and postsetal lamellae enclosing setal fascicles (Fig. 3B, C), these continuing in some form through posterior segments; notopodial lamellae eventually becoming more elongate, somewhat triangular (Fig. 3D); neuropodial lamellae remaining broadly rounded throughout.

Dorsal branchiae first present from setiger 2 (Fig. 3A), with those of setigers 2–4 fused basally to modified notopodia, subsequent dorsal branchiae fused to presetal lamellae; anterior dorsal branchia thickened (Fig. 3B), then becoming triangular and thinner posteriorly (Fig. 3C, D); dorsal branchiae relatively short for first 45–50 setigers, never reaching even half of distance to dorsal midline (Fig. 3A), thereafter branchiae becoming thinner, longer, extending to dorsal midline. Ventral branchiae beginning from about setiger 55 as extensions of postsetal lamellae, remaining relatively short (Fig. 3C), until about setiger 100–125, then becoming longer, more cylindrical; in far posterior segments, nearly reaching ventral midline, but never as long as dorsal branchiae (Fig. 3D).

Notosetae of setigers 2–4 modified into cluster of about 20 heavy spines (Fig. 3A); subsequent notosetae numerous, thin capillaries until about setiger 75 where 5–8 hooded hooks appear; capillaries become heavier and more limbate in far posterior segments; individual notopodial hooks strongly curved, with pointed main fang surmounted by several minute teeth (Fig. 3F, G). Anterior neurosetae include row of 25–30 heavy spines, thin companion capillaries, and ventral bundle of thin capillaries (Fig. 3B); neuropodial spines each with smooth shaft that tapers abruptly, then con-

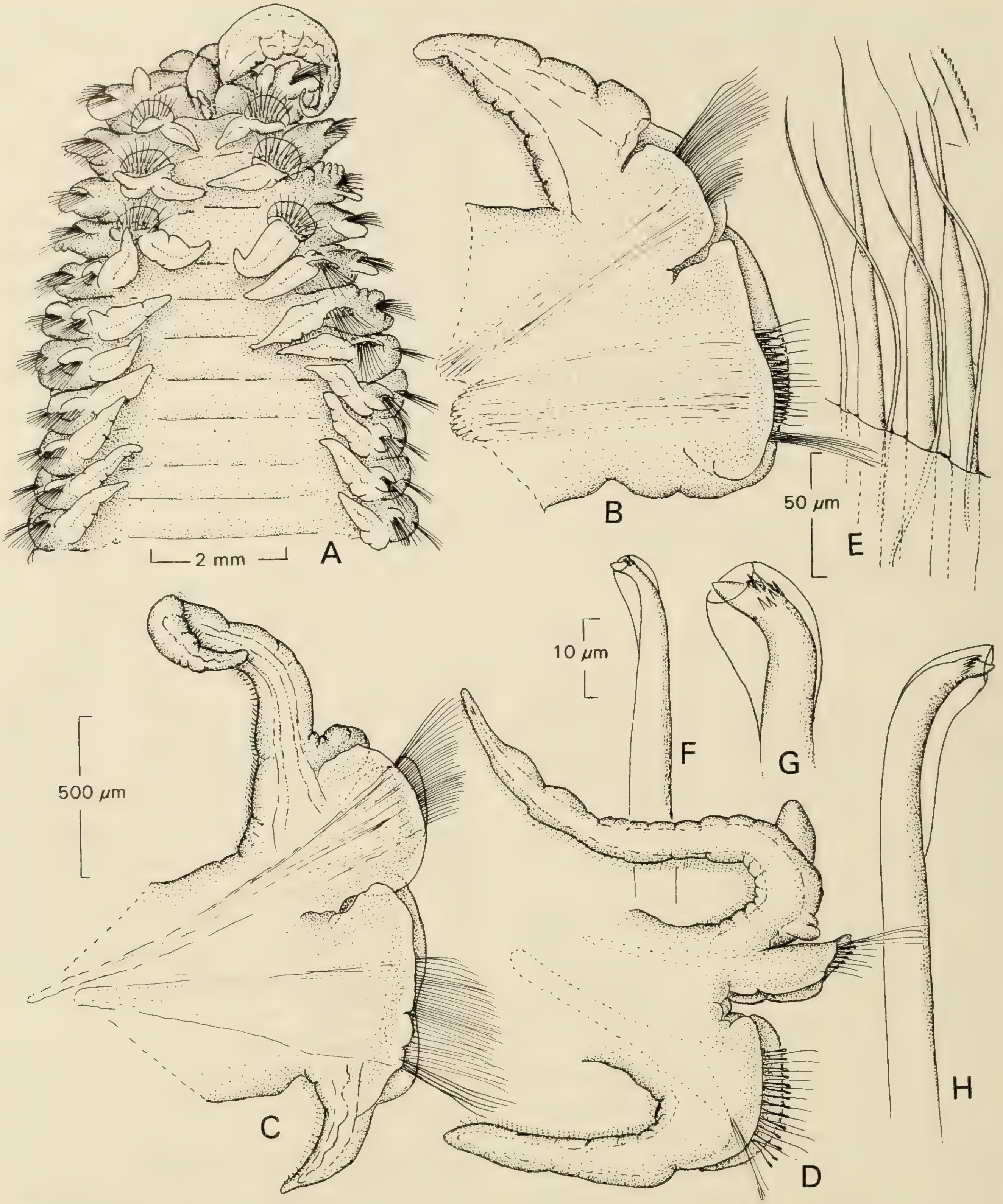

Fig. 3. *Lindaspio southwardorum* (USNM 148674). A, Anterior end, dorsal view; B, Anterior parapodium, anterior view; C, Middle parapodium, anterior view; D, Posterior parapodium, anterior view; E, Modified anterior neurosetae and accompanying capillaries; F–G, notopodial hooded hooks; H, neuropodial hooded hook.

tinues as fine, pointed tip with fine serrations or bristles sometimes visible along edge (Fig. 3E); spines present until about setiger 40, then replaced by thin capillaries; these capillaries accompanied by delicate neuropodial hooded hooks from about setiger 75 (Fig. 3H); each hook smaller, more delicate than notopodial hook; each hook with several minute teeth above main fang. Details of multidentate hooded hooks cannot be resolved by light microscopy.

Etymology.—The specific name honors Drs. Eve C. and Alan J. Southward, deep-sea biologists of the Plymouth Laboratory, United Kingdom. The Southwards participated in the collection of this species and provided field observations.

Remarks.—*Lindaspio dibranchiata* and *L. southwardorum* are the only spionids known to have ventral branchiae and dorsal rosettes or clusters of spines in some anterior notopodia. These characters are considered to be species-level rather than generic characters because of the unusual habitat of these species. A related species described as *Scolecolepides caruncidatus* from off North Carolina has been reexamined and is referred to *Lindaspio.* This latter species lacks ventral branchiae and the dorsal modified spines, but has the same generic-level features including branchiae from setiger 2 and anterior modified neuropodial spines. *L. carunculata* has a distinctive caruncle that is narrow and undulating; *L. southwardorum* has a similar, but smaller caruncle, whereas *L. dibranchiata* has only a short, mound-like caruncle.

Lindaspio carunculata (Maciolek, 1984), new combination

Fig. 4

Scolecolepides carunculatus Maciolek, 1984: 58–61, figs. 5–6.

Material examined.—Off North Carolina, U.S. Atlantic Slope and Rise Program, Station 2, 34°14.9′N, 75°43.6′W, 1000 m, 27 Mar 1984, 2 specimens (USNM 148675–148676).

Description.—Large anterior fragment 15 mm long, 2.8 mm wide for 52 setigerous segments; small, nearly complete specimen, 4.6 mm long, 0.7 mm wide for 47 segments. Body very broad anteriorly, with branchiae of anterior segments short, leaving dorsum completely uncovered; posteriorly, body narrower, branchiae longer, covering much of body surface; individual segments of middle and posterior segments each with distinct medial ciliary band. Color in alcohol: brownish yellow, with branchiae and parapodial lamellae white.

Prostomium button-shaped, prolonged anteriorly into 2 prominent lobes, continuing posteriorly as narrow, undulating caruncle to middle of setiger 2 (Fig. 4A); eyes and occipital tentacle absent. Peristomium reduced, fused with setiger 1; palps short, curved, tapering to narrow tip. Pygidium unknown.

Setiger 1 reduced, lacking notosetae; notopodia limited to thin lamellae thought to be branchiae in original description (Fig. 4A); neuropodia with rounded lamellae and fascicle of capillary setae. Setiger 2 shifted dorsally, following segments normally oriented, with prominent notopodial and neuropodial pre- and postsetal lamellae encompassing fascicles of setae (Fig. 4B). Notopodia of anterior segments with low, rounded presetal lamella and larger, postsetal lamella fused to branchiae; notopodial lamellae becoming thinner, more membranous posteriorly, and separating from branchiae (Fig. 4C, D). Neuropodia of anterior setigers with setae completely enclosed by pre- and postsetal lamellae, with those of anterior segments having low, rounded margins, becoming triangular posteriorly. Branchiae first present from setiger 2; anterior branchiae cirriform, fused for half their length to postsetal notopodial lamellae; branchiae of middle and posterior segments larger, thin, lamellate, free from notopodial lamellae, or fused only at base, each ciliated along inner border, merging with dorsal, transverse ciliary band.

Notosetae of anterior and middle segments all smooth capillaries, arranged in 3–4 rows with longest setae in superior bundle; notopodial hooded hooks first present from setiger 42 (21 in small specimen); each hook very narrow, with curved tip and no apparent apical teeth above main fang (Fig.

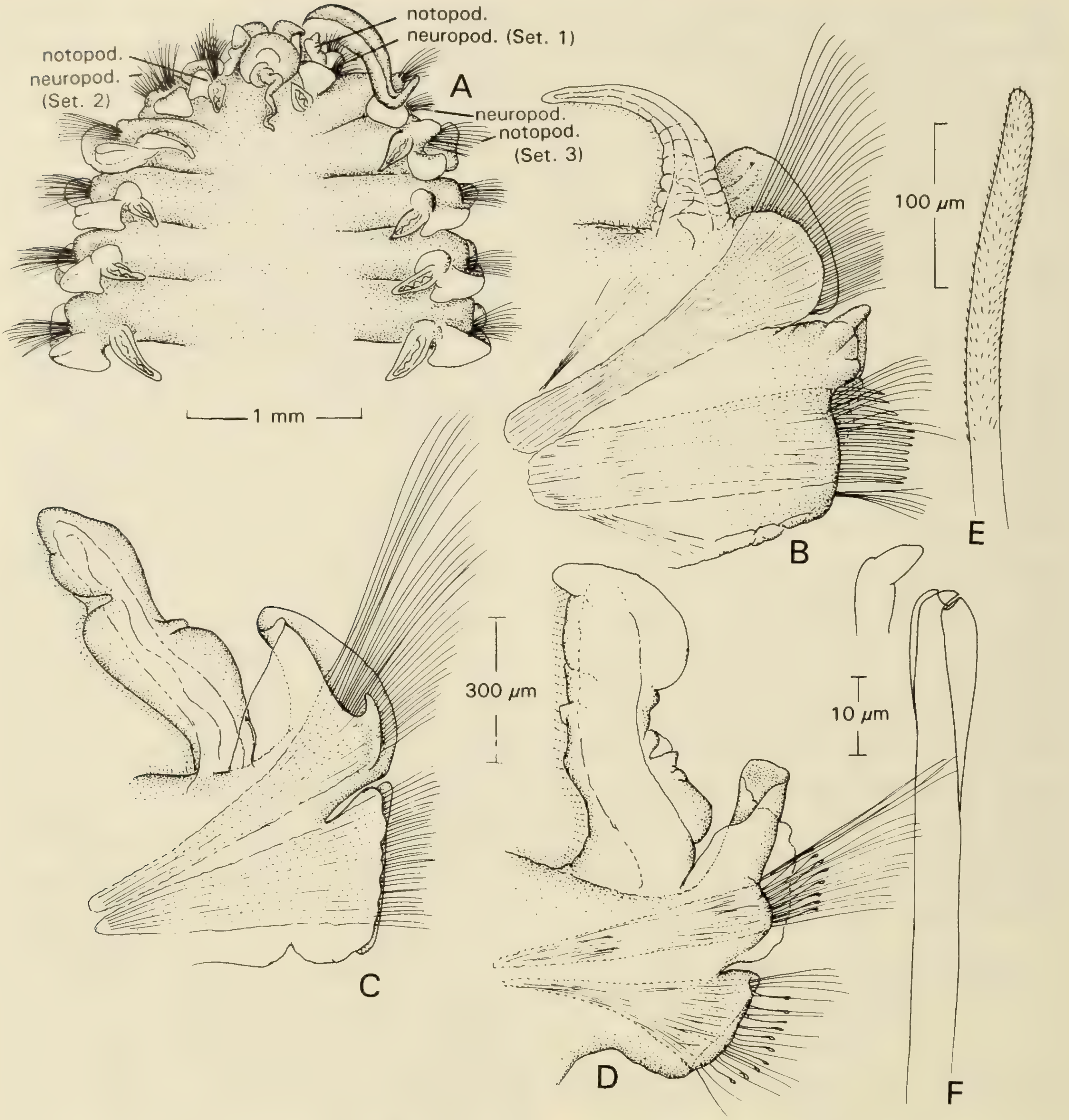

Fig. 4. *Lindaspio carunculata* (USNM 148675). A, Anterior end, dorsal view; B, Anterior parapodium, anterior view; C, Middle parapodium, anterior view; D, Posterior parapodium, anterior view; E, Modified anterior neuroseta; F, Neuropodial hooded hook. Abbreviations: notopod. (=notopodium); neuropod. (=neuropodium); Set. (=setiger).

4F); hooks numbering about 15 in fascicle, accompanied by numerous thin capillaries. Neuropodia of setigers 1–2 with dense fascicles of capillaries, partially replaced by heavy modified hirsute spines from setiger 3 (Fig. 4E), continuing until about setiger 12, then spines becoming thinner, and replaced entirely by capillaries again from setiger 15; spines blunted when worn (Fig. 4E); pointed when unworn (Maciolek, 1984: fig. 6C); neuropodial hooded hooks first present from about setiger 29 (10 in small specimen); hooks of same structure as notopodial hooks, numbering about 11 per fascicle with 20 or more accompanying capillaries.

Remarks.—This redescription of *Lindaspio caruncúlata* elucidates the structure and distribution of the hooded hooks and presents a reinterpretation of the nature of the first setiger. In the original account, the neuropodia were said to be lacking, with only notopodia and small branchiae present (Maciolek 1984). It is now clear that the structures thought to be branchiae are actually notopodial lamellae situated adjacent to the dorsally placed neuropodia. Branchiae actually begin on setiger 2. With this interpretation, the species does not agree with the definition of *Scolecolepides* in which branchiae begin on setiger 1. Hooded hooks were lacking in all of the specimens on which the original description was based (Maciolek 1984). With the information presented here about the structure of the hooded hooks, the nature of the prostomium and caruncle, and the reduced nature of setiger 1, it is apparent that *S. carunculatus* is closely related to the two new deep-sea hydrothermal vent species assigned to the new genus *Lindaspio.* On this basis, *S. carunculatus* is herein referred to *Lindaspio,* despite the lack of ventral branchiae and modified anterior notosetae. These characters, while unique in the Spionidae, are considered to be species-level rather than generic characters.

Discussion

Two related genera, *Marenzelleria* Mesnil and *Scolecolepides* Ehlers, were revised by Maciolek (1984). The new genus, *Lindaspio,* represents a deep-sea companion to the shallow water *Scolecolepides.* A unifying feature of these two genera is the presence of ventral acicular spines in some anterior setigers. A distinguishing feature that separates these genera is the presence of branchiae on setiger 1 in *Scolecolepides* and setiger 2 in *Lindaspio.*

The three species of *Lindaspio* described in the present paper represent two species groups. The first, represented by *L. carunculata,* is the least modified and is found in ambient soft-bottom sediments on the continental slope off North Carolina. The second group, represented by *L. dibranchiata* and *L. southwardorum,* comes from sediments associated with active hydrothermal vents in the eastern Pacific. The presence of anterior notopodial spines and ventral branchiae is highly diagnostic and unique among spionids. It is likely that the branchiae are an adaptation that provides an increased respiratory surface in a low-oxygen environment. The function of the anterior spines is not known. The close relationship between the less modified *L. carunculata* and the two vent species is seen in the structure of the prostomium and the caruncle. All three species have well-developed frontal lobes or horns. The narrow, undulating caruncle of *L. carunculata* was noted by Maciolek (1984) to be an unusual character that was more reminiscent of amphinomids. The presence of a similar caruncle in one of the vent species, *L. southwardorum,* and similar prostomia in all three species, is evidence of their close relationship.

Lindaspio southwardorum at a length of 15+ cm and a width of 7 mm is one of the largest and most robust spionids ever reported. The presence of fragments of an even larger specimen indicate that this species can reach proportions that are gigantic for a spionid.

Acknowledgments

We are grateful to Drs. J. Frederick Grassle and Verena Tunnicliffe for providing the Guaymas Basin and Juan de Fuca specimens, respectively, for study. Drs. Eve C. and Alan J. Southward participated in the collection of the Juan de Fuca species and provided notes on color. The specimens from off North Carolina were collected as part of a biological reconnaissance of the U.S. South Atlantic continental slope and rise by the U.S. Department of the Interior, Minerals Management Service under contract No. 14-12-0001-30064. Financial support for the publication of this paper was generously provided by Science Applications International Corporation.

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DELTAMYSIS HOLMQUISTAE, A NEW GENUS AND SPECIES OF MYSIDACEA FROM THE SACRAMENTO-SAN JOAQUIN ESTUARY OF CALIFORNIA (MYSIDAE: MYSINAE: HETEROMYSINI)

Thomas E. Bowman and James J. Orsi

Abstract.—*Deltamysis holmquistae* is described from the Sacramento-San Joaquin estuary of central California. Its sparsity in plankton net samples suggests that its supposed habitat has not been sampled adequately. Limited sampling in tule beds failed to take specimens. *Deltamysis holmquistae* may be an introduced species; it was not found until 1977 despite sampling for Mysidacea in the estuary since 1963. Characteristics of the tribe Heteromysini are redefined to include *Deltamysis.* The new definition allows the addition of *Burrimysis* and the transfer of *Mysidetes* from the Leptomysini to the Heteromysini. A new key to the Heteromysini is given which includes the subgenera of *Heteromysis.*

W. M. Tattersall (1932) identified the following five species of Mysidacea taken on the 1912–1913 *Albatross* survey of San Francisco and San Pablo Bays: *Neomysis mercedis* Holmes, 1897; *Neomysis franciscorum* Holmes, 1900 (current name *N. rayi* (Murdoch, 1885)); *Neomysis kadiakensis* Ortmann, 1908; *Neomysis costata* (Holmes, 1900) (misidentification of species currently named *Exacanthomysis davisi* (Banner, 1948)); *Neomysis macropsis* Tattersall, 1932 (current name *Alienacanthomysis macropsis* (Tattersall, 1932)).

Most numerous of these species is *N. mercedis,* which is usually most abundant in Suisun Bay and the Sacramento-San Joaquin River delta upstream from San Pablo Bay (Orsi & Knutson 1979). The new species described below occurs in the same area as *N. mercedis.*

Methods

The California Department of Fish and Game has conducted a continuous monitoring survey of zooplankton since June 1968. Mysids were collected in a 0.505 mm mesh plankton net, 1.48 m long and 29 cm in diameter. Diagonal 10-minute bottom to surface tows were made at fixed stations in Suisun Bay, the Delta and, during periods of high river outflow, downstream into San Pablo Bay (Fig. 1). Sampling was done twice a month from April to November and monthly in March and November. Year-round sampling was done prior to 1984. Surface and bottom electrical conductivity, surface temperature, chlorophyll *a,* and Secchi disc measurements were made at the beginning of each tow.

Heteromysini Hansen 1910

Deltamysis, new genus

Scale of antenna 2 with transverse suture separating short distal segment. Pereopod 2 (endopod of thoracopod 3) not stouter than other pereopods. Pleopods rudimentary in both sexes. Endopod of uropod without spines near statocyst or on medial margin. Penis of moderate size, reaching distal margin of basipod of pereopod 7. Telson entire,

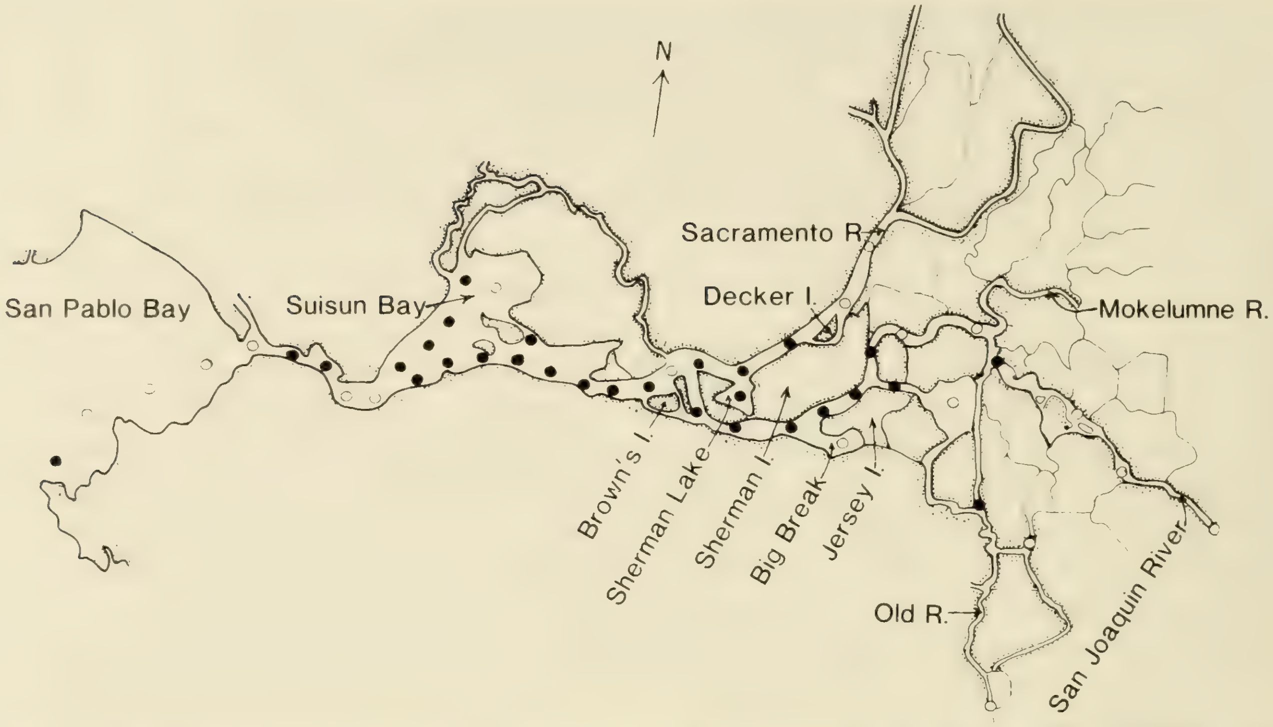

Fig. 1. Sacramento-San Joaquin Estuary. Zooplankton stations of California Department of Fish and Game indicated by circles. Stations where *Deltamysis holmquistae* has been collected indicated by solid circles.

apex with pair of short central spines flanked by 3 pairs of longer spines.

Type species.—*Deltamysis holmquistae,* new species.

Etymology.—From the Sacramento-San Joaquin *Delta* + *mysis.*

Deltamysis holmquistae, new species
Figs. 2–4

Material.—All from the Sacramento-San Joaquin Estuary, collected between Brown's Island and Jersey Island (Fig. 1) and deposited in the Division of Crustacea, Smithsonian Institution. Holotype ♂, USNM 251607. Allotype ♀, USNM 251608. Paratypes: USNM 251609, 5; USNM 251610, 7; (exact locations and dates of collection unknown for USNM 251607-251610). USNM 251611, Sta. 78, between Sherman I. and Jersey I., 2 Sep 1977, 1 ♀; USNM 251612, Sta. 78, 26 Aug 1977, 2; USNM 251613, Sta. D-11, Sherman Lake, 18 Aug 1977, 2; USNM 251614, Sta. 76, W of Jersey I., 26 Aug 1977, 2; USNM 251615, Sta. 74, S of Sherman Lake, 2 Sep 1977, 1; USNM 251616, Sta. 62, N of Sherman Lake, 1 Sep 1977, 1; USNM 251617, Sta. D-15, between Sherman I. and Jersey I., 26 Aug 1977, 2; USNM 251618, Sta. 56, N of Brown's I., date unknown, 9.

Etymology.—Named for the distinguished Swedish zoologist, Charlotte Holmquist, in recognition of her important contributions to the systematics of Mysidacea of the North American Pacific coast.

Description.—Length of adult (rostrum-telson) 3–5 mm. Carapace emarginate posteriorly, exposing pereonite 7. Rostrum short, rounded in dorsal view, pointed in lateral view. Eyestalks short, about as long as eye, which is about 1.5× as wide as long and born obliquely laterad on stalk. Telson about 1.2× as long as width at base, entire, with 7 pairs of marginal spines as follows: 4–5 lateral pairs increasing in length posteriorly, 2 long subapical pairs, and 1 short apical pair less than half length of subapical spines.

Antenna 1 peduncle segments 1 and 3 subequal in length, about 2× as long as seg-

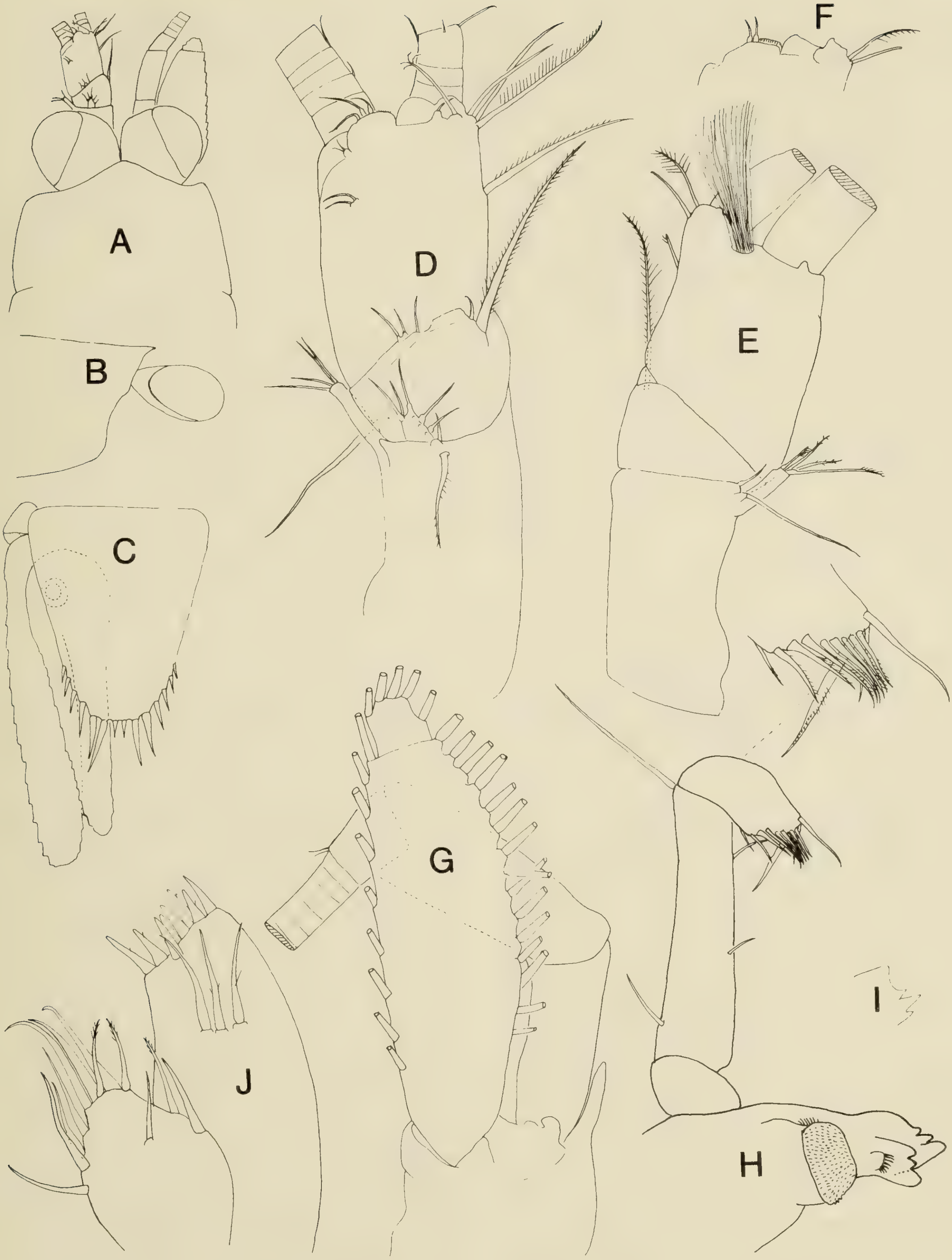

Fig. 2. *Deltamysis holmquistae*: A, Anterior body, dorsal, ♀; B, Same, lateral; C, Telson and uropod, dorsal, ♂; D, Left antenna 1, dorsal, ♀; E, Left antenna 1, ventral, ♂; F, Antenna 1, distal part of segment 3, dorsal, ♂; G, Left antenna 2, dorsal, ♂; H, Left mandible, anterior, ♂; I, incisor of right mandible, ♂; J, Left maxilla 1, posterior, ♂.

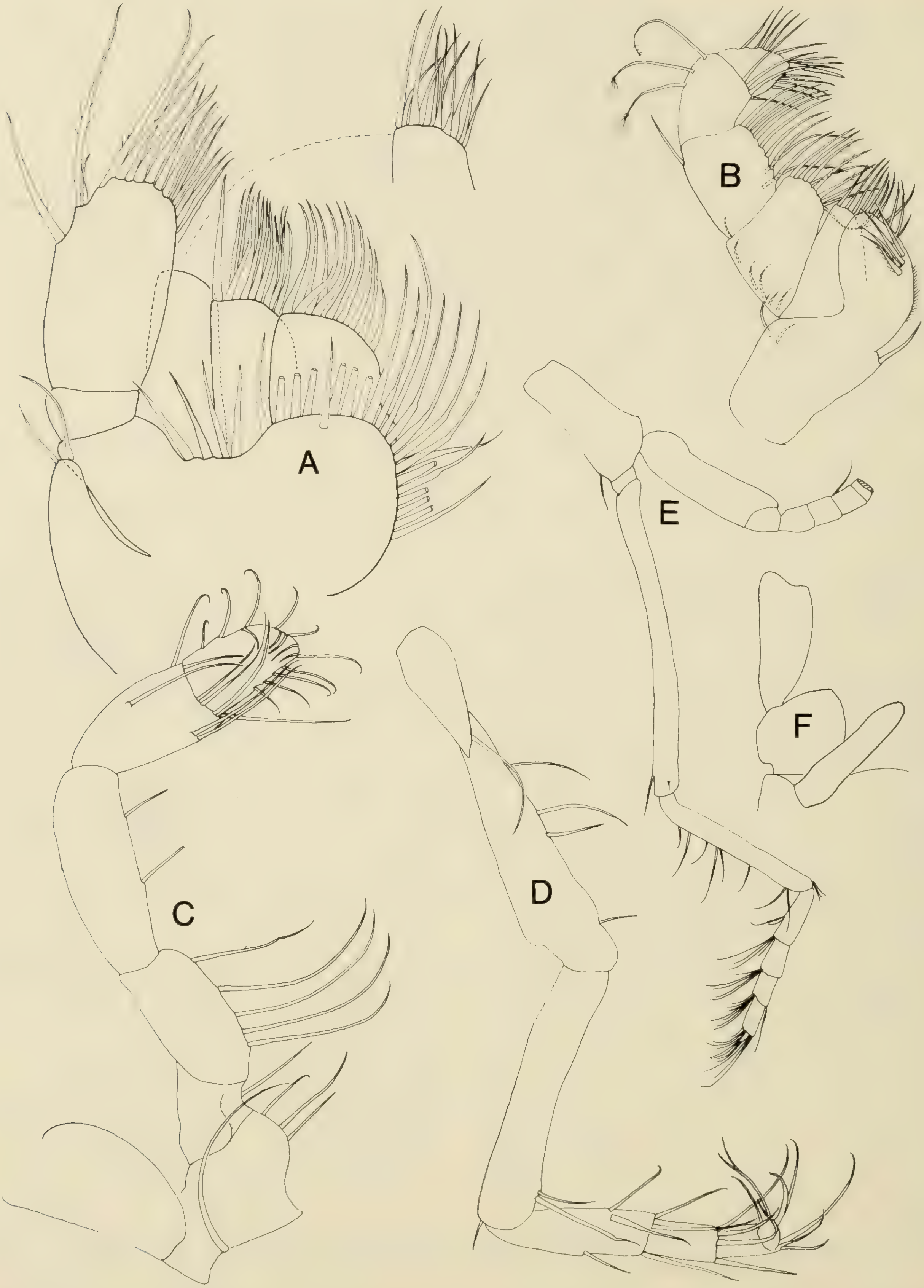

Fig. 3. *Deltamysis holmquistae*: A, Left maxilla 2, anterior, ♂; B, Left maxilliped, anterior, ♂; C, Left pereopod 1, ♀; D, Pereopod 3; E, Pereopod 7, ♀; F, Pereopod 7 basipod and 1st segment of exopod, ♂, with penis at base.

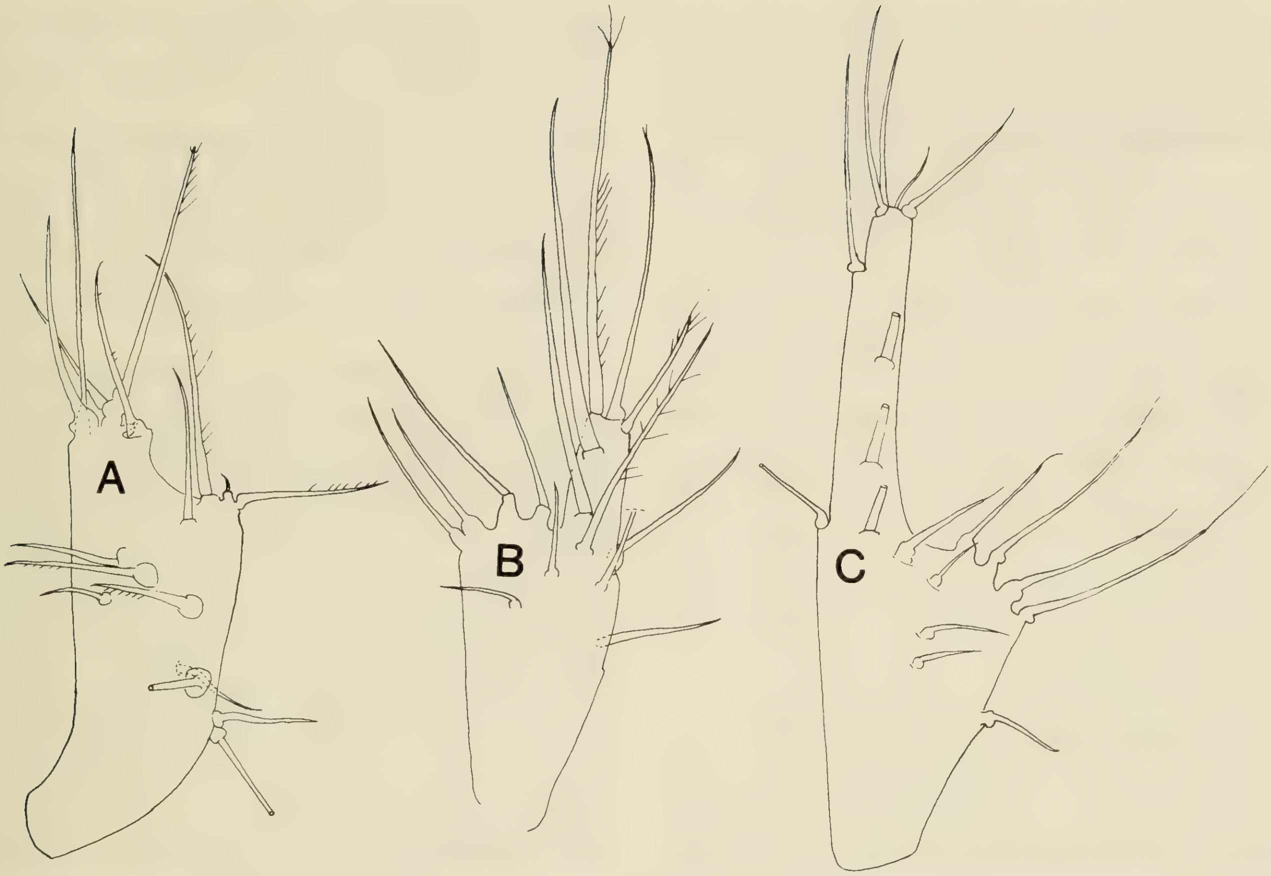

Fig. 4. *Deltamysis holmquistae*: A, Left pleopod 1, anterior, ♂; B, Left pleopod 4, posterior, ♂; C, Right pleopod 5, anterior, ♂.

ment 2. Segment 1 with long middorsal seta near distal margin, subtriangular process distally slightly lateral to seta bearing several bulbous-based setae, and narrow rectangular process at distolateral corner bearing 4 apical setae. Segment 2 with dorsal distomedial seta reaching almost to distal end of segment 3. Segment 3 with several rounded setose lobes dorsally at distal end; male antennular brush inserted directly on ventral surface, male lobe not developed.

Antenna 2 peduncle reaching distal end of scale; segment 1 produced at distomedial corner into lanceolate process. Scale about 3× as long as wide; distal segment about 0.1× scale length.

Left mandible with 3-cuspate incisor and lacinia; right mandible with 4-cuspate incisor and no lacinia. Spine-row represented by 8 slender spines on a rounded boss. Molar with broad elliptical grinding surface. Palp segment 2 about twice length of segment 3, with seta on distolateral corner more than half length of segment; segment 3 with oblique distal margin armed with row of setae of uniform length and 2 longer setae.

Maxilla 1 outer ramus with 9 apical spines and 3 surface setae. Inner ramus with 11 marginal setae and 1 surface seta.

Maxilla 2 protopod inner margin completely covered with setae. Endites densely setose apically. Endopod proximal segment less than 0.25× as long as distal segment; latter almost 2× as long as wide, densely setose at and near apex. Exopod not reaching proximal margin of segment 1 of endopod, armed only with 2 apical setae.

Maxilliped (endopod of thoracopod 1) endite of basis nearly reaching distal margin of ischium. Medial margin of all segments except propus densely setose; latter with 3 setae on medial part of distal margin and 3 broom setae on lateral margin.

Pereopod 1, merus with 5 long setae on

anterior margin; carpus with 2 shorter setae on anterior margin; propus with 6 long setae on or near distal margin and 3 on lateral surface; dactyl about 0.8 × length of propus, with 15 marginal setae. Pereopods 2–3, "tarsus" of 3 segments. Pereopods 4–7, "tarsus" of 4 segments.

Penis cylindrical, about 5 × as long as wide, reaching slightly beyond basis of pereopod 7, unarmed.

Pleopods of both sexes in form of unsegmented plates. Proximal part bearing bulbous-based setae; pseudobranchial lobe also bearing bulbous-based setae. Distal part short in pleopods 1–4, in pleopod 5 longer and armed with long setae on anterior surface and at apex.

Uropod about 1.7 × length of telson. Exopod slightly longer than endopod.

Relationships.—Definitions of the Heteromysini, e.g., that of Tattersall & Tattersall (1951), emphasize the enlarged pereopod 2, the rudimentary condition of the pleopods in both sexes, the long penes, and the reduction in size of the male lobe of antenna 1 and in the number of setae borne by this lobe.

However, in the genus *Harmelinella* Ledoyer (1989), recently described and assigned to the Heteromysini, pereopod 2 is not enlarged. In other features *Harmelinella* conforms to the Heteromysini except for the very long male pleopod 3, comparable in length to the long pleopod 4 characteristic of members of the tribe Mysini. If *Harmelinella* is accepted in the Heteromysini, enlargement of pereopod 2 is no longer a requirement for membership in this tribe, and *Deltamysis* can be included in it without difficulty, as can *Burrimysis* Jaume & Garcia (1992), which also lacks an enlarged pereopod 2.

The genus *Mysidetes* Holt & Tattersall (1906) does not have an enlarged pereopod 2, but the pleopods of both sexes are rudimentary, and the penes are very long, in some species extending anterior to the rostrum. The male lobe varies from small to well developed. *Mysidetes* is now placed in the tribe Leptomysini, in which it is the only genus with rudimentary pleopods in both sexes. If the definition of the Heteromysini is expanded to accommodate *Harmelinella* and *Deltamysis,* then *Mysidetes* must be transferred from the Leptomysini to the Heteromysini.

Some characters of *Mysidella* Sars (1872) fit the revised definition of *Heteromysis* given below, including the rudimentary pleopods of both sexes and the long penes. However, the form of the labrum, mandible, and maxilla 2 of *Mysidella* are so unusual that it is generally assigned to its own subfamily, *Mysidellinae* Czerniavsky, 1882.

Within the expanded Heteromysini *Deltamysis* is most similar to the recently described *Burrimysis* Jaume & Garcia (1992), from an anchialine lake in a cave of the island of Cabrera, Balearic Islands. Whether or not the features that distinguish *Burrimysis* from *Deltamysis* are of generic value is debatable, but for now we prefer to recognize both genera pending further evidence. *Burrimysis* differs from *Deltamysis* in having a telson with an apical cleft lined with denticles, a uropodal endopod with a spine on the medial margin near the statocyst and a row of spines on the lateral margin, and an unsegmented antennal scale.

An alternative to expanding the limits of the Heteromysini would be to resurrect Holt & Tattersall's (1906) subfamily Mysidetinae, but with tribal rank, Mysidetini, to include *Mysidetes, Harmelinella, Deltamysis,* and *Burrimysis.* Hansen (1910) rejected "the subfamily Mysidetinae which I cannot accept" without a word of explanation of his reasons for doing so, and assigned *Mysidetes* to the Leptomysini. All subsequent authors, including Tattersall (1955) have followed Hansen in placing *Mysidetes* in the Leptomysini.

Although a plausible case can be made for recognizing the Mysidetini, we choose for the time being to expand the definition of the Heteromysini and to postpone consideration of the validity of the Mysidetini.

We offer the following revised diagnosis of the Heteromysini and key to the genera and subgenera assigned to it. The section of the key dealing with the subgenera of *Heteromysis* is modified from Băcescu (1968).

Tribe *Heteromysini* Norman, 1892

Male lobe of antenna 1 usually reduced. Antenna 2 scale setose all around. Pereopod 2 sometimes enlarged and robust. Propus (=carpopropodus of Hansen and others) of pereopods 3–7 divided into subsegments. Pleopods of both sexes rudimentary, except long pleopod 3 of male *Harmelinella*. Penes long, cylindrical. Telson with or without apical cleft.

Key to the Genera and Subgenera of Heteromysini

1. Pereopod 2, some of distal segments enlarged 2
– Pereopod 2 without enlarged distal segments 4
2. Body isopod-like, dorsoventrally flattened. Pleonites with well developed pleurae .... *Platymysis* Brattegard, 1980
– Body not dorsoventrally flattened. Pleonites without well developed pleurae 3
3. Eye reduced, restricted to distolateral part of eyestalk .... *Heteromysoides* Băcescu, 1968
– Eye well developed, occupying full width of distal part of eyestalk.... .... *Heteromysis* Smith, 1873
  a. Pereopod 2 very robust, greatly inflated; merus enlarged, dentate; exopod reduced. Endopod of uropod longer than exopod .... *H.* (*Gnathomysis*) Bonnier & Pérèz, 1902
  – Pereopod 2 only moderately robust. Endopod of uropod shorter than exopod .... b
  b. Pleopods not sexually dimorphic. Pleon with median sternal processes .... *H.* (*Heteromysis*) Smith, 1873
  – Pleopod 4 sexually dimorphic. Pleon without median sternal processes c
  c. Antenna 1 with pair of modified setae on distomedial corner of segment 3; medial seta linguiform with subterminal flagellum; lateral seta simple, very long, directed laterally .... *H.* (*Olivemysis*) Băcescu, 1968
  – Antenna 1 with 2 pairs of simple setae on distomedial corner of segment 3, pairs diverging from each other. Pleopod 4 with 2 apical setae longer than pleonite 4 *H.* (*Neoheteromysis*) Băcescu, 1976
4. ♂ pleopod 3 very long, 2-segmented .... *Harmelinella* Ledoyer, 1989
– ♂ pleopod 3 rudimentary, unsegmented.................... 5
5. Telson with apex truncate, not cleft .... *Deltamysis,* new genus
– Telson with apical cleft lined with denticles 6
6. Endopod of uropod with row of spines on medial margin (except *M. hanseni* Zimmer, 1914). Antennal scale with small distal segment separated by transverse suture (except *M. halope* O'Brien, 1986) .... *Mysidetes* Holt & Tattersall, 1906
– Endopod of uropod without row of spines on medial margin. Antennal scale without suture .... *Burrimysis* Jaume & Garcia, 1992

Occurrence of *Deltamysis holmquistae*

Although there has been continuous sampling for zooplankton in the estuary since June 1968 and earlier sampling from 1963–

1965 (Turner & Heubach 1966, Heubach 1969), *Deltamysis* was not found until August 1977. It has been collected every year since 1977, but in low numbers, from one specimen in 1984 to 39 in 1987. Specimens have been taken from western San Pablo Bay (one specimen during the high spring outflow of 1983) to Decker Island in the Sacramento River, in the San Joaquin River to the mouth of the Mokelumna River, and in the southern delta from the Old River (Fig. 1). The salinities where it was found ranged from fresh water to 18.7‰. Most specimens have been taken in salinities of 1.1–2.2‰, which is at the upstream edge of the entrapment or null zone, a region of high turbidity, long water residence time, and high concentrations of phytoplankton and zooplankton.

Heteromysini are epibenthic or commensal rather than planktonic, and plankton tows collect them neither efficiently nor quantitatively. Commensal species, summarized by Mauchline (1980), are associated with sponges, sea anemones, gastropod shells of hermit crabs, and brittle stars. Almost nothing is known about the habits of species of Heteromysini that have not been found to be commensal. In the living coral reef exhibit at the National Museum of Natural History, Smithsonian Institution, a population of *Heteromysis mayana* Brattegard (1970) lives in the lagoon part of the exhibit. Individuals swim constantly among the sea grass plants at the bottom, alighting briefly on the grass leaves from time to time, but not swimming into the water column above the leaves. If *Deltamysis holmquistae* behaves like *Heteromysis mayana*, plankton tows would capture few of them, and the low numbers in the Department of Fish and Game samples are the result of a sampling method that is inefficient for this species. Sampling with a net mounted on a sled would produce better information on the distribution and abundance of *D. holmquistae*.

We have considered the possibility that *Deltamysis* lives in the extensive tule marshes of the estuary. These are marshes dominated by the large sedges *Scirpus lacustris* and *S. acutus*. These marshes are of two kinds, seasonally flooded and permanently flooded. The extensive marshes north of Suisun Bay fall in the first category. These marshes are owned either by the state of California or by private hunting clubs which flood them, usually in September, to attract waterfowl. No aquatic animals can survive year-round in these marshes because they are drained in the spring.

The tule marshes that are permanently underwater are more limited in area. The largest are on Brown's Island and at the submerged western end of Sherman Island around Sherman Lake. Sampling on Brown's Island with a dip net failed to catch mysids. Sherman Lake has a regular sampling station, but only one *Deltamysis* specimen has been caught there in all the years of sampling. At another station surrounded by submerged tule marsh in Big Break, no *Deltamysis* specimens have ever been taken.

Origin of *Deltamysis*

Deltamysis holmquistae could be native to the Sacramento-San Joaquin Delta and overlooked until recently because of inadequate sampling techniques. Or it could be an addition to the growing list of species considered to have been introduced through human activity (e.g., Orsi et al. 1983, Ferrari & Orsi 1984, Orsi & Walter 1991). San Francisco Bay is young, formed in the late Pleistocene (Atwater et al. 1977), hence there has been insufficient time for endemic species to evolve in its estuarine habitats. These habitats have been available since the arrival of Spanish ships in 1776 for colonization by non-endemic species, many of which were introduced during the last century (Carlton 1979).

If *D. holmquistae* is an introduced species, there is no evidence of its possible origin, since no mysid species closely resembling it is known elsewhere. Since several copepods introduced into the Sacramento-San Joaquin estuary are considered to be native to the Far East, that is the obvious geographical region in which to begin to search for *Deltamysis.*

Acknowledgments

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DIASTYLOPSIS GOEKEI, A NEW SPECIES (CRUSTACEA: CUMACEA: DIASTYLIDAE) FROM ANTARCTIC WATERS

Daniel Roccatagliata and Richard W. Heard

Abstract.—Specimens of *Diastylopsis goekei,* n. sp. were collected at depths ranging from 2 to 399 m in the Weddell Sea, the Ross Sea, and along the Antarctic Peninsula. *Diastylopsis goekei* is most closely related to two other Subantarctic-Antarctic species, *Diastylopsis annulata* (Zimmer, 1902) and *D. dentifrons* (Zimmer, 1903). *Diastylopsis goekei* can be distinguished from these and all other members of the genus by the following combination of characters: (1) carapace with 8–9 transverse ridges, (2) ocular lobe with 2 teeth, (3) first and second ridges with a row of mid-dorsal teeth (absent in adult male), (4) second ridge with a tooth on each side of frontal lobe, (5) pseudorostral lobes with an arch of teeth, appearing as a conspicuous lateral serration when viewed dorsally, and (6) telson longer than the peduncle of the uropod. The taxonomic status of several species of the genus *Diastylopsis* is briefly discussed.

The genus *Diastylopsis* contains nine species (Jones 1969), all recorded from latitudes greater than 30°, both in the northern and southern hemispheres (eastern and western North Pacific, Magellan Strait, New Zealand, Subantarctic Islands, and Antarctica). This paper deals with the description of a new species collected on the continental shelf and slope of eastern Antarctica.

Many specimens used in this study were obtained during the Antarctic cruises of the research vessels *Eltanin, Glacier,* and *Hero* between 1962–1982 and made available through the Smithsonian Oceanographic Sorting Center. Additional specimens were taken during the Argentine Antarctic Survey of 1990.

The types and other specimens utilized in the present study have been deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN) and the National Museum of Natural History, Smithsonian Institution (USNM).

In this paper the term "adult female" refers to a female with fully developed oöstegites, "preparatory female" to a female with incipient oöstegites long enough to meet at the mid-ventral line, "adult male" to a male with fully formed pleopods, "preparatory male" to a male with developing pleopods, "juvenile" to a female or male in an early stage of development, and "manca" to a specimen lacking the last pair of peraeopods.

Diastylopsis goekei, new species
Figs. 1–4

Type material.—Holotype, adult ♀ (MACN 33440). Type locality: "Caleta Potter," "Isla 25 de Mayo" (King George Island), Antarctic Peninsula, 2 m, Aug 1990, Light trap. Paratypes from the same locality: 1 adult ♀, 3 juveniles (MACN 33441); 1 adult ♀, 1 adult ♂, 3 juveniles (USNM 251917).

Additional material examined.—Antarctic Peninsula: *Eltanin* Cr. 6, St. 408 (61°16′S, 56°11′W, 223–225 m, 31 Dec 1962, Menzies trawl): 1 adult ♀, 5 juveniles. *Eltanin* Cr. 6, St. 410 (61°18′–61°20′S, 56°09′–

56°10′W, 220–240 m, 31 Dec 1962, Blake trawl): 1 adult ♀. *Eltanin* Cr. 6, St. 437 (62°50′–62°51′S, 60°35′–60°40′W, 267–311 m, 9 Jan 1963, Blake trawl): 1 juvenile. *Eltanin* Cr. 6, St. 439 (63°50′–63°51′S, 62°35′–62°38′W, 128–165 m, 9 Jan 1963, Blake trawl): 1 juvenile. *Eltanin* Cr. 12, St. 1003 (62°41′S, 54°43′W, 210–220 m, 15 Mar 1964, Blake trawl): 2 juveniles. *Hero* Cr. 691, St. 23 (64°11.3′–64°12.1′S, 62°39.6′–62°40′W, 93–95 m, 9 Feb 1969, Try net): 1 preparatory ♀. *Hero* Cr. 824, St. 3 (65°14′S, 64°15.5′W, 56–60 m, 15 Mar 1982, Van Veen grab): 1 preparatory ♀, 2 juveniles. *Hero* Cr. 824, St. 28 (64°13.8′–64°14.2′S, 62°34.1′–62°35.1′W, 70–98 m, 24 Mar 1982, Blake trawl): 1 juvenile. A sample taken by the "Instituto Antártico Argentino" at "Caleta Potter," "Isla 25 de Mayo" (King George Island), 2 m, Aug 1990, Light trap: 6 adult ♀♀, 1 preparatory ♀, 22 juveniles. Ross Sea: *Eltanin* Cr. 51, St. 5761 (76°01.5′–76°01.6′S, 179°49.9′–179°53.5′E, 388–399 m, 8 Feb 1972, Menzies trawl): 2 adult ♀♀, 1 preparatory ♀, 2 preparatory ♂♂, 10 juveniles, 2 mancas. *Eltanin* Cr. 51, St. 5762 (76°02.1′–76°02.3′S, 179°52.1′–179°57′W, 347–358 m, 9 Feb 1972, Menzies trawl): 1 preparatory ♀, 7 juveniles, 1 manca. Weddell Sea: *Glacier* Cr. 2, St. 0009 (77°54.2′S, 45°13.3′W, 252 m, 3 Mar 1969, Anchor dredge): 1 juvenile.

Diagnosis.—Carapace with 8–9 transverse ridges, first and second ridges with row of mid-dorsal teeth (absent in adult male), second ridge with 1 tooth on each side of frontal lobe; ocular lobe with 2 teeth; pseudorostral lobes with arch of teeth, appearing as conspicuous lateral serration when viewed dorsally. Telson of adult female slightly longer than peduncle of uropod, with 9–12 spines on each side. Telson of adult male distinctly longer than peduncle of uropod, with 20–21 spines on each side. Uropodal endopod of adult female with 7–9, 3–4, and 2 spines on inner margin of articles 1–3, respectively. Uropodal endopod of adult male with 20–21, 10 and 6 spines on inner margin of articles 1–3, respectively.

Description.—Adult female: Length: 7.6–8.9 mm (from tip of pseudorostrum to end of telson). Integument thin and translucent. Carapace (Fig. 1A, B) slightly more than one fourth total length, width 0.7–0.8 times of length, and slightly greater than or equal to depth; with 8–9 transverse ridges (see also Fig. 4): first weakly developed, reduced to row of mid-dorsal teeth behind ocular lobe and ill-defined line on pseudorostral lobes; second complete, with row of mid-dorsal teeth and 1 tooth on each side near frontal suture; third complete, laying just behind frontal lobe, sometimes with several incipient mid-dorsal teeth; fourth not reaching dorsal mid-line of carapace; fifth complete; sixth–eighth interrupted dorsally, eighth frequently weak and broken, or absent; ninth complete, running parallel to posterior and postero-lateral margins of carapace. Ocular lobe lacking eyes, about 0.5 times as long as pseudorostrum, armed with 2 teeth. Pseudorostral lobes with arch of teeth, appearing as conspicuous lateral serration when viewed dorsally. Antennal notch rounded; antero-lateral angle with acute tooth; antero-ventral margin of carapace armed with row of teeth decreasing in size posteriorly.

Thorax typical of genus, varying between 0.8–1.0 times of carapace length depending on degree of overlap in segments.

Abdomen less than 0.5 times combined lengths of carapace and thorax; first segment without sternal tooth; fifth distinctly longer than others.

Telson (Fig. 3A) slightly more than 1.5 times length of sixth abdominal segment; armed with 9–12 spines laterally and 2 stout spines terminally, terminal spines slightly longer than posterior lateral spines.

First antenna (Fig. 1C). Peduncle, first article slightly longer than second and third combined; second article slightly longer than

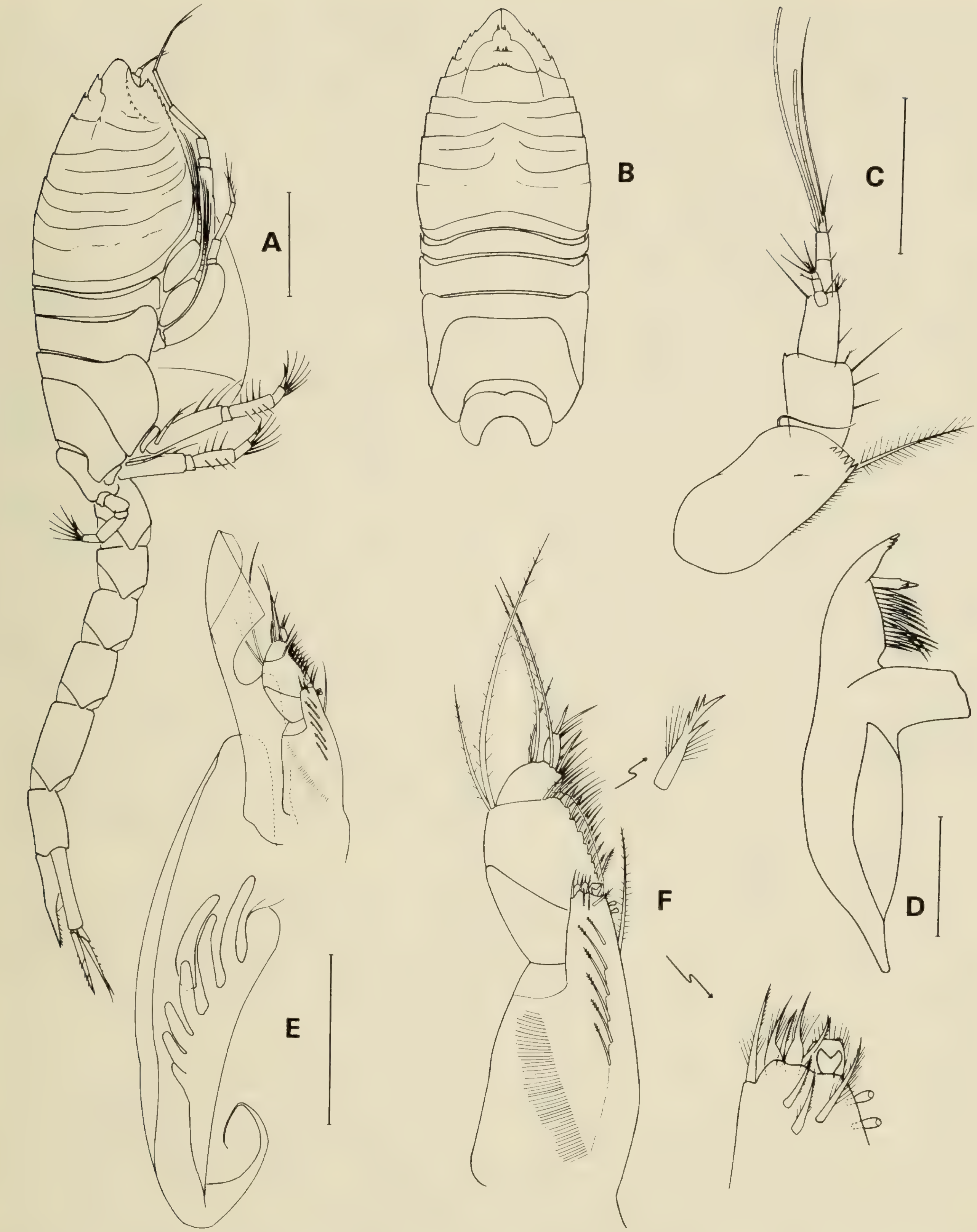

Fig. 1. *Diastylopsis goekei,* n. sp. Adult ♀: A, lateral view. B, dorsal view of carapace and thorax. C, first antenna (right). D, mandible (left). E, first maxilliped (left). F, details of first maxilliped endite. Scales = 1 mm for A–B (same scale); 0.2 mm for C–D; 0.5 mm for E.

third. Both flagella 3-articulate; accessory flagellum almost as long as proximal article of main flagellum.

Mandible (Fig. 1D) with 13–14 serrate spines between the incisor and molar processes.

First maxilliped (Fig. 1E, F). Basal process as illustrated, characterized distally by 2 broad-based setae, 1 short, thick lobe (all three furnished with setules), and 1 bifid, refringent body. Carpus, inner margin with numerous setae and row of characteristic spines (see spine enlarged in illustration).

Second maxilliped (Fig. 2A). Basis robust, about one third longer than combined lengths of other articles; inner distal margin with 5–6 stout plumose setae, outer distal margin with 4–5 less well-developed, slightly bipectinate setae. Ischium unarmed, distinct from dorsal view, but almost imperceptible ventrally. Carpus longer than combined lengths of propodus and dactylus, with approximately 8 plumose setae on inner margin and 2 on outer distal margin. Oöstegite bearing 12–15 setae.

Third maxilliped (Fig. 2B). Basis more than twice as long as combined lengths of other articles, inner margin with plumose setae and distal row of denticles; external distal process weakly developed, bearing 4–5 plumose setae. Ischium and merus with plumose setae and serrations distally. Carpus with plumose setae, inner margin with 4 denticles increasing in size distally. Propodus and dactylus with simple or weakly plumose setae, denticles absent.

First peraeopod (Fig. 2C) extending beyond the tip of pseudorostrum by length of dactylus. Basis about 0.8–0.9 times as long as combined lengths of other articles; both margins with plumose setae; distally with 1 short simple seta on ventral face and long plumose setae on dorsal face; denticles occurring on ventral face, both distally and on row parallel to outer margin. Ischium and merus, combined lengths equal to propodus, both articles with denticles distally and 1 small simple seta on inner margin. Carpus, propodus, and dactylus elongate, bearing simple setae; carpus about 0.2 times longer than propodus and 0.1 times longer than dactylus.

Second peraeopod (Fig. 2D). Basis about 0.9 times of combined lengths of other articles, inner margin with numerous plumose setae and 1 distal spine, outer margin with 1 distal plumose seta. Merus with 1 distal spine and 1 plumose seta on inner and outer margins, respectively. Carpus about 0.9 times of combined lengths of ischium and merus, with 4–5 distal spines. Propodus and dactylus with simple setae, combined lengths about 0.2 times longer than carpus.

Third peraeopod (Fig. 2E). Basis, length approximately equal to combined lengths of ischium, merus, and carpus; with numerous plumose and simple setae. Remaining articles with simple setae only. Carpus about 0.4 times as long as merus. Propodus slightly shorter than dactylus. Exopod rudimentary, composed of 2 articles.

Fourth peraeopod similar to third except basis approximately same length as ischium and merus combined, carpus about 0.5 times as long as merus, some differences in setation.

Fifth peraeopod (Fig. 2F) similar to third except basis approximately the same length as merus, carpus approximately two thirds as long as merus, exopod lacking, some differences in setation.

Uropod (Fig. 3A). Peduncle, slightly shorter than telson, inner margin with 10–12 spines. Rami subequal, about 0.70–0.75 times as long as peduncle. Endopod, articles decreasing in length distally; first article slightly longer than other two combined, with 7–9 spines on inner margin and 1 seta on outer margin; second with 3–4 spines on inner margin and 2 setae on outer margin; third with 2 spines on inner margin, 2 setae on outer margin, and 1 spine (slightly shorter than article) distally. Exopod, first article with 1 small seta on outer margin, second

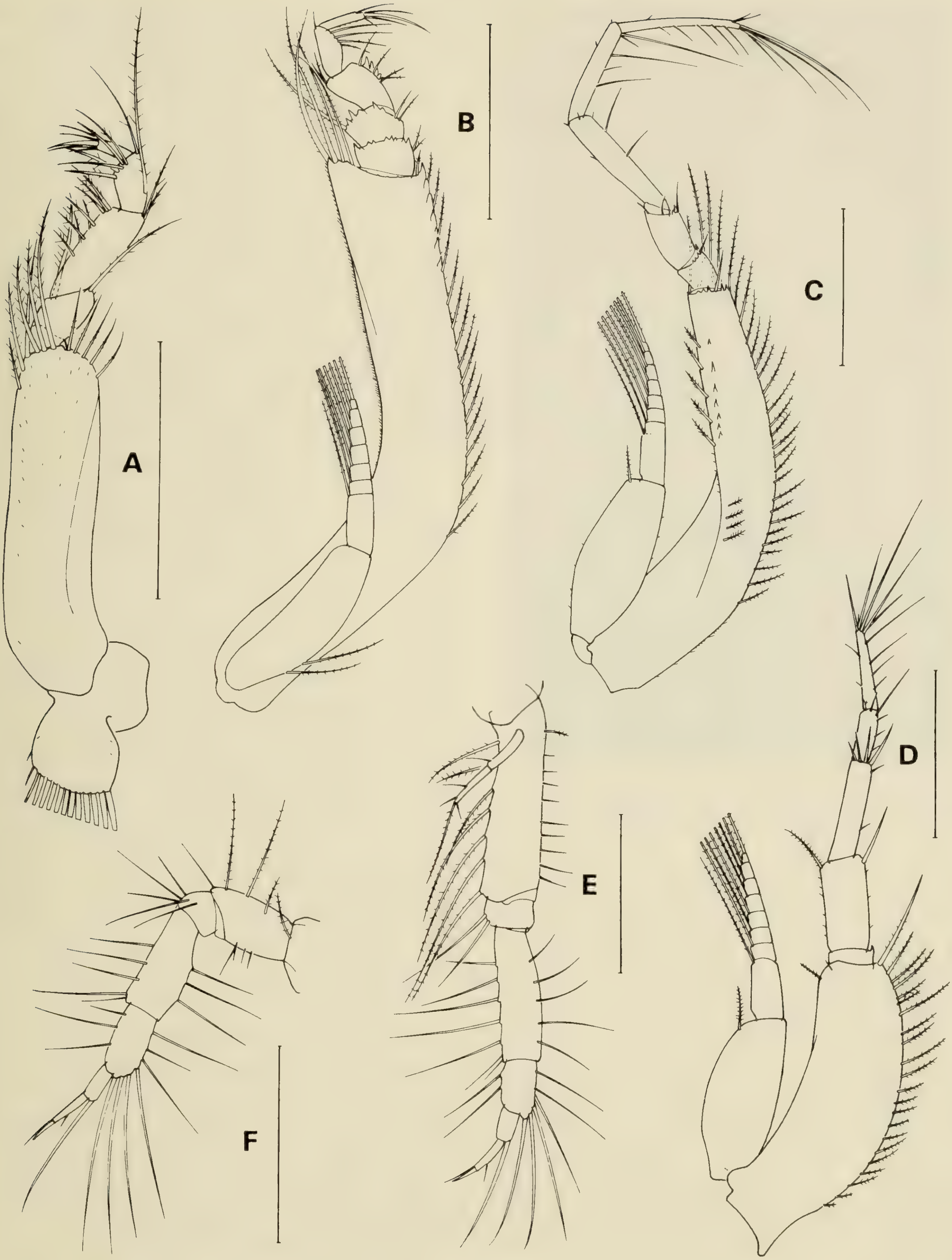

Fig. 2. *Diastylopsis goekei,* n. sp. Adult ♀: A, second maxilliped (left). B, third maxilliped (right). C, first peraeopod (right). D, second peraeopod (left). E, third peraeopod (left). F, fifth peraeopod (left). Scales = 0.5 mm.

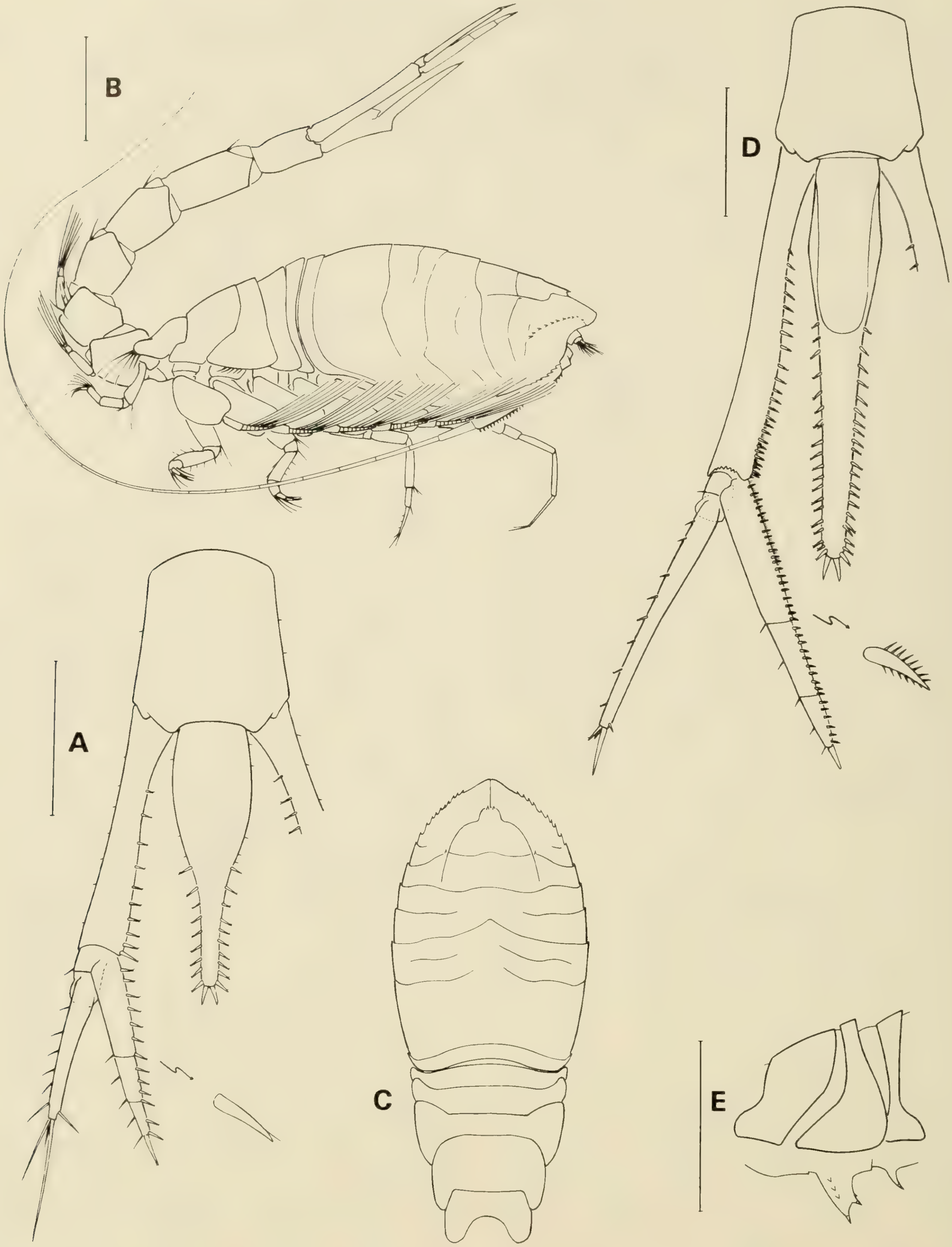

Fig. 3. *Diastylopsis goekei,* n. sp. Adult ♀: A, telson and uropod (left). Adult ♂: B, lateral view. C, dorsal view of carapace and thorax. D, telson and uropod (left). Juvenile: E, thoracic segments 2–4 (peraeopods omitted). Scales = 0.5 mm for A, D–E; 1 mm for B–C (same scale).

article with numerous setae, viz., 10–13 irregularly alternating on dorsal and ventral outer margins (only dorsal ones drawn), 1 subterminal on inner margin, and 3 unequal terminal (longest seta somewhat shorter than second article).

Adult male.—Length: 9.3 mm (from tip of pseudorostrum to end of telson).

In addition to sexual differences in the development of the antenna, exopods, and pleopods, the adult male differs from the adult female by the following characters:

Carapace (Fig. 3B, C) approximately 0.3 times total length; anterior part wider in dorsal view. First and second ridges without row of mid-dorsal teeth; eighth ridge absent. Antennal notch less pronounced; anterolateral angle rounded.

Thorax approximately two thirds as long as carapace.

Telson (Fig. 3D) approximately 2.5 times as long as sixth abdominal segment, approximately as long as fifth and sixth segments combined; armed with 20–21 spines on each side and 2 stout spines terminally, terminal spines clearly longer than posterior lateral spines; pre-anal region with mid-dorsal depression bounded by sharp carina.

Uropod (Fig. 3D). Peduncle, approximately 0.8 times as long as telson, inner margin with 24–26 pectinate spines. Rami 0.80–0.85 times as long as peduncle. Endopod, inner margin of articles 1–3 with 20–21, 10 and 6 pectinate spines, respectively; distal end, spine about 0.5 times as long as the third article. Exopod: second article, outer margin with setae becoming spines distally (14–15 in total; only dorsal ones drawn), inner margin with 1 subterminal spine, distal end with 3 unequal spines (longest spine approximately 0.2 times as long as second article). All exopod spines nonpectinate. Other appendages were not examined to avoid destroying the only adult male available.

Juvenile and preparatory instars.—(Fig. 3E). Second thoracic sternite of males with spiniform projection (rudimentary in adult males, absent in all female stages). Third thoracic sternite in both sexes with prominent mid-ventral projection armed with 1–3 medial and 0–3 lateral spines; projection more developed in males than in females (rudimentary in adult males, absent in adult females).

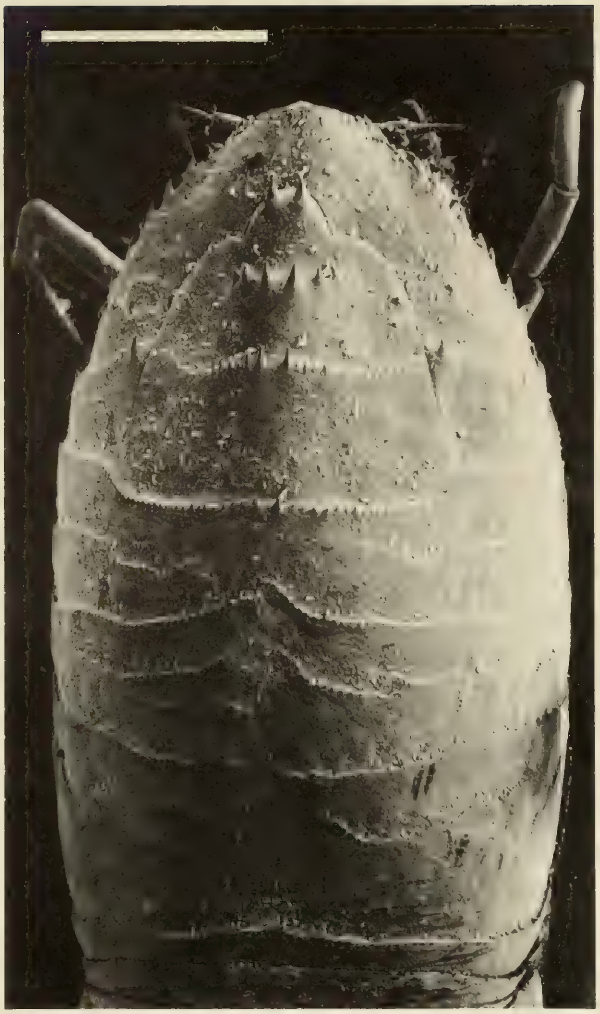

Fig. 4. *Diastylopsis goekei,* n. sp. Juvenile: Scanning electron micrograph of carapace. Scale = 0.5 mm.

Variation.—Slight deviations in the general pattern of the ridges of the carapace were observed.

Etymology.—The species is named in honor of Gary D. Goeke for his help in the initial stages of our study and in recognition of his contributions to carcinology.

Remarks.—*Diastylopsis goekei, D. annulata* (Zimmer, 1902), and *D. dentifrons* (Zimmer, 1903) are distinguished from all other members of the genus by having 8–9 transverse ridges on the carapace and the telson equal to or longer than the peduncle of the uropod. *Diastylopsis annulata* and *D. dentifrons* have an anterior mid-dorsal carina bearing three large, forwardly directed teeth on the frontal lobe. This feature was confirmed by the examination of a juvenile from South Georgia Island (USNM 251933) and some of the females and juveniles from Kerguelen Islands reported by Ledoyer (1977). *Diastylopsis goekei* is easily distinguished from *D. annulata* and *D. dentifrons* by having (1) carapace without a mid-dorsal carina, (2) two transverse rows of teeth on frontal lobe (absent in adult male), and (3) an arch of teeth on pseudorostral lobes, appearing as a conspicuous lateral serration when viewed dorsally. To clearly establish differences in the chaetotaxy and proportions of the articles of the appendages, more complete descriptions based on adult specimens from the type localities of *D. annulata* and *D. dentifrons* are necessary.

Diastylis anderssoni Zimmer, 1907 (type locality South Georgia Island) resembles *Diastylopsis goekei, D. annulata,* and *D. dentifrons* by the presence of numerous transverse ridges on the carapace and a rudimentary exopod on the third and fourth peraeopods of the female. *Diastylopsis goekei* can be distinguished from *Diastylis anderssoni* by possessing the third and fourth thoracic segments more produced posteriorly, a smaller size, and a telson which extends beyond the uropodal peduncle (in *D. anderssoni* the telson is distinctly shorter than the uropodal peduncle).

Discussion.—Jones (1969) listed the following species of *Diastylopsis* Smith, 1880: *D. dawsoni* Smith, 1880 (North Pacific); D. *tenuis* Zimmer, 1936 (Southern California); *D. elongata* Calman, 1911, *D. crassior* Calman, 1911, and *D. thileniusi* (Zimmer, 1902) (New Zealand); *D. robusta* (Zimmer, 1902) (Magellan Strait); *D. annulata* (Zimmer, 1902), *D. dentifrons* (Zimmer, 1903), and *D. diaphanes* Zimmer, 1907 (Subantarctic and/or Antarctic waters). More recently, Băcescu (1982), based on a typographic error, introduced the name *Diastylopsis bosphorica* in his description of a new species belonging to *Diastyloides* Sars, 1900.

There are several unresolved taxonomic problems involving some of the species of *Diastylopsis.* Zimmer (1907, 1913) presented a brief description of *D. diaphanes* based on a manca collected off western Antarctica and its taxonomic position remains questionable.

The description of *D. annulata* was based on two juvenile females from South Georgia Island (Zimmer 1902, 1909), and that of *D. dentifrons* on two females (both with fully developed oöstegites?) and two juvenile males, all from the Kerguelen Islands (Zimmer 1903, 1908, 1913). Later, Hale (1937) examined a large series of *Diastylopsis* from Heard Island and described the adult female and the juvenile male stages. Based on his observations, he regarded the specimens of this series as intermediate between *D. annulata* and *D. dentifrons* and considered the latter as a junior synonym of the former. This designation has been followed by Lomakina (1968), Jones (1971), and Ledoyer (1974, 1977). However, we believe that until adult specimens of *D. annulata* from South Georgia are available, this synonymy cannot be confirmed.

Derjavin (1926) described *Diastylopsis calmani* from the western North Pacific, but Lomakina (1958) considered this species as a "forma" of the type species, *D. dawsoni* Smith, 1880, which was originally described from the eastern North Pacific. Lomakina's opinion was also followed by Gamô (1965, 1968). We believe that a careful comparison of eastern and western North Pacific specimens is required to justify this nomenclatural change.

Day (1980) transferred *Diastylopsis thileniusi* to the genus *Dic* Stebbing, 1910. This species is in an intermediate position between both genera. *Dic thileniusi* has, like the other three members of the genus *Dic,* a third maxilliped with a greatly expanded ischium. However, it differs from these three species by having the third and fourth thoracic segments markedly produced posteriorly, which is characteristic of the genus *Diastylopsis.*

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REMARKS ON DISTRIBUTION AND HOSTS FOR SYMBIOTIC CRUSTACEANS OF THE MEXICAN PACIFIC (DECAPODA AND ISOPODA)

Ernesto Campos, Alma Rosa de Campos, and Jorge Ramirez

Abstract.—Updated information on the distribution, hosts, synonymy and taxonomy is given for six Mexican Pacific crustacean species. These include the caridean shrimp of the family Palaeomonidae, *Pontonia pinnae*; the brachyuran crabs of the family Pinnotheridae, *Dissodactylus lockingtoni, Opisthopus transversus, Parapinnixa affinis*; and the isopods of the families Cymothoidae, *Lironeca menziesi*; and Bopyridae, *Progebiophilus bruscai.*

Resúmen.—Se actualiza la información sobre distribución, huéspedes, sinonímia y taxonomía para seis especies de crustáceos de la costa del Pacífico de México. Estas incluyen un camarón carideo de la familia Palaeomonidae *Pontonia pinnae,* tres cangrejos braquiuros de la familia Pinnotheridae *Dissodactylus lockingtoni, Opisthopus transversus, Parapinnixa affinis*; y los isópodos de las familias Cymothoidae, *Lironeca menziesi* y Bopyridae, *Progebiophilus bruscai.*

Among the most conspicuous symbiotic crustaceans inhabiting the Mexican Pacific waters are brachyuran crabs, caridean shrimps and isopods. Pinnotherid crabs in particular are typically found living symbiotically (Schmitt et al. 1973). These crabs have recently been the target of several systematic and ecological studies (Campos-González 1986; Campos-González & Campoy-Favela 1987b; Campos 1989a, 1989b, 1990; Campos & Griffith 1990). Among caridean shrimps, Palaeomonids (*Pontonia* spp.) and Alpheids (*Betaeus* spp.) have frequently been observed in association with bivalve and gastropod molluscs (Hart 1964; Wicksten 1983, 1989; Campos-González 1988). In the eastern Pacific taxonomic and ecological studies of isopods such as the Cymothoidae, parasitic on fishes, or the Epicaridea (Bopyridae, Cryptoniscidae and Entoniscidae) parasitic on crustaceans, include Brusca (1980), Kuris et al. (1980), Campos-González et al. (1986), Campos-González & Campoy-Favela (1987a), and Campos & Campos, (1989, 1990).

The present note updates information on the distribution and taxonomy for six Mexican symbiotic crustaceans and their hosts. Results are based on collections made in the Baja California peninsula during 1987 to 1990. The localities "La Bajada," "El Rincón," and "Punta de Sofía" are in Bahía Tortugas, Baja California Sur. The material studied has been deposited at the Laboratory of Invertebrates of the Facultad de Ciencias, Universidad Autónoma de Baja California. The synonymy, except for the isopods, is restricted.

Family Palaeomonidae
Pontonia pinnae Lockington, 1878

Pontonia pinnae.—Holthuis 1951:118, pl. 36, figs. a-l.—Brusca 1980:250, fig. 14.5.—Wicksten 1983:10, 18; 1989:17, 19.—Campos-González 1988:384-385.

Distribution and hosts.—Upper Gulf of California to Panama, and west coast of Baja California Sur to San Ignacio Lagoon; in the bivalves *Pinna rugosa* Sowerby and *Atrina tuberculosa* (Sowerby).

Material examined and new record.—1 male, 4 juveniles, La Bajada Beach (27°41′N, 114°52′W), 30–31 Dec 1990, in *Atrina tuberculosa.*

Remarks.—Two species of pen-shells were collected in the above locality, *Pinna rugosa* (1 specimen) and *Atrina tuberculosa* (about 100 specimens) which represent a range extension for both bivalve species. Their known range now includes the Gulf of California to Panama, and the west coast of Baja California Sur to Bahía Tortugas. The pen-shells were collected in a semi-protected rocky beach consisting of a mixture of sand, mud, gravel and pebbles. All pen-shells had fully developed gonads indicating sexual activity. Although *Pontonia pinnae* was found in *A. tuberculosa* only, this shrimp is most commonly found commensally with *P. rugosa* at Bahía de los Angeles, Baja California (Campos-González 1988).

Family Pinnotheridae

Dissodactylus lockingtoni Glassell, 1935

Dissodactylus lockingtoni Glassell, 1935: 100, pl. 27, figs. 5–8, text-fig. 68.—Griffith 1987a:2292–2310; 1987b:401, 413, 419, figs. 8B, 9B, 11B, 13B, 14B.

Dissodactylus smithi Rioja, 1944:149, figs. 1–6, 11–15.

Distribution and hosts.—Gulf of California; San Felipe, Baja California and Puerto Peñasco, Sonora. Whether *D. lockingtoni* ranges throughout the Gulf of California as stated by Glassell (1935), has not been established; symbiont on the echinoids *Encope californica* Verril, *E. grandis* L. Agassiz, *E. micropora* L. Agassiz, and presumably *Mellita longifissa* Michelin.

Material examined and new host.—A total of 663 specimens (including megalopae, juveniles, males and females), Campo El Pescador, on coast 4.5 km north of San Felipe, Baja California (31°04′11″N, 114°50′22″W); Jan–Dec 1989; symbiont in *Mellita grantii* Mortensen.

Remarks.—Based on a collection from the upper Gulf of California (around San Felipe), Glassell (1935) determined *Mellita longifissa* as one of four hosts of *Dissodactylus lockingtoni.* An examination of several hundred host specimens from the vicinity of San Felipe agreed well with the diagnostic features given by Harold & Telford (1990) for *Mellita grantii.* They pointed out that the test of *M. grantii* has its maximum thickness anterior to the anal lunule, and that the periproct is located anterior to the same lunule (Fig. 1A). In contrast, the test of *M. longifissa* has the highest point more anteriorly and the anal lunule is confluent with the periproct (Fig. 1B). Mortensen (1948), Durham (1961) and Ebert & Dexter (1976) also recognized the distinctness of these two species. In a morphometric analysis, Ebert & Dexter pointed out that the ratios length/width of the test, width/length of the anal lunule, and anal lunule length/total length are useful in differentiating *M. grantii* from *M. longifissa.* Our morphometric analysis on one hundred specimens of *M. grantii* identified using Harold & Telford (1990), indicates that the above ratios actually overlap with those of *M. longifissa* (Table 1). Relative size ratios, therefore, do not appear to be useful in the identification of these two closely related species.

The status of *M. longifissa* in the Gulf of California (Brusca 1980, Caso 1961, Pohle 1989) needs to be re-assessed using the identification criteria of Harold & Telford.

Opisthopus transversus Rathbun, 1893

Opisthopus transversus Rathbun, 1893:252; 1918:172–174, pl. 27, figs. 4–5, text-fig. 110.—Beondé 1968:375–377.—Schmitt et al. 1973:7–12, 14, 131–132.—Garth & Abbott 1980:618.

Distribution and hosts.—From Monterey, California, U.S.A., to Laguna de San Ig-

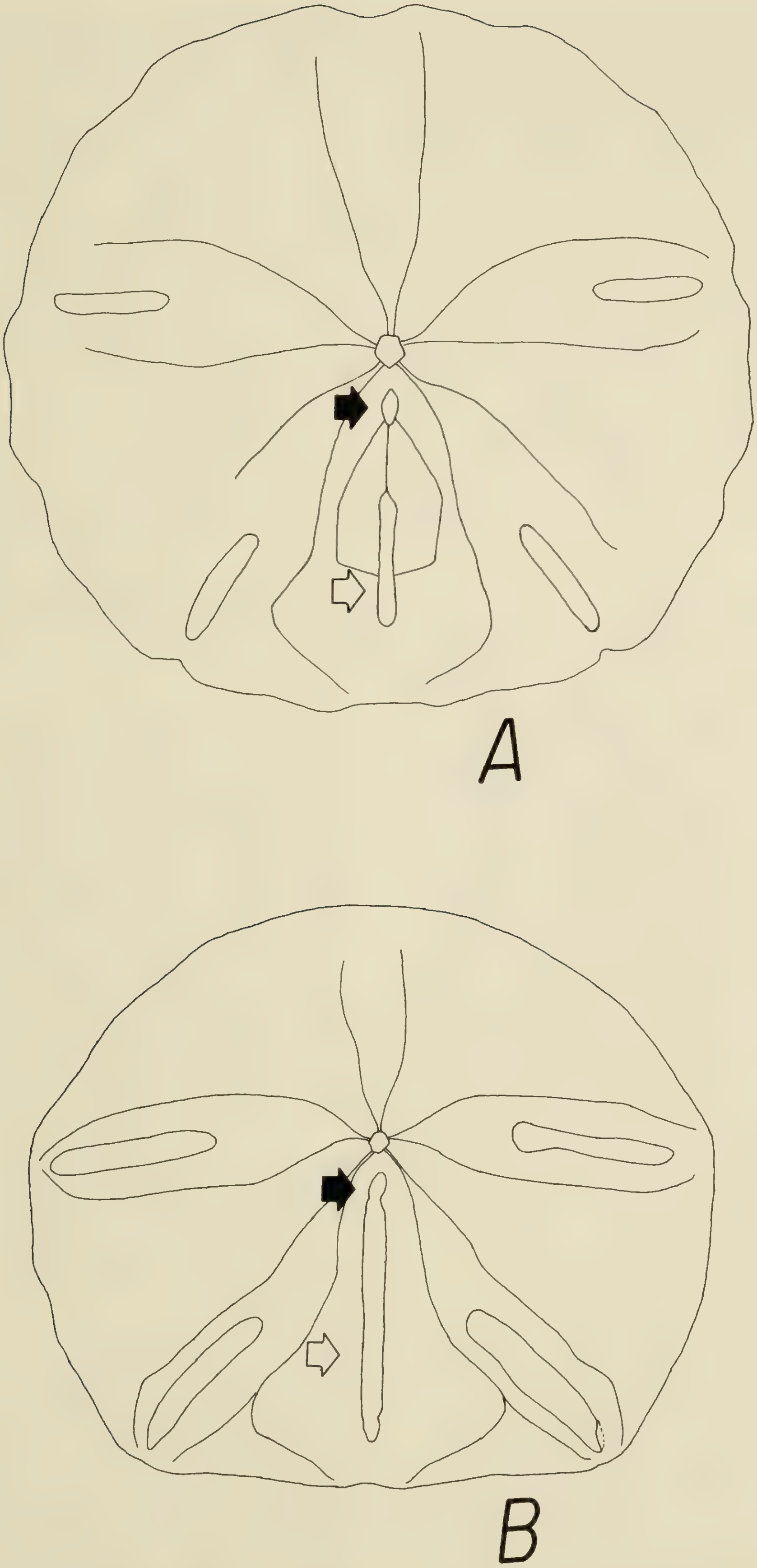

Fig. 1. Oral view of the sand-dollar: A, *Mellita grantii* Mortensen; B, *Mellita longifissa* Michelin. Black arrows indicate the periproct, white arrows the anal lunule.

Table 1.—Comparison of three morphometric ratios of *Mellita longifissa* and *M. grantii.* Total length (TL) cross parallel to anal lunule (=5I lunule); total width is perpendicular to the TL in the widest point. Data in A and B are from Ebert & Dexter (1976). *SD* = Standard deviation. Measurements are in mm.

Ratio		Species	*n*	Range	Mean	*SD*
Length/width	A	*M. longifissa*	24	0.73–0.85	0.81	0.026
	B	*M. grantii*	28	0.90–0.99	0.95	0.020
	C	*M. grantii*	100	0.72–1.38	0.94	0.070
Lunule 5I Width/length	A	*M. longifissa*	24	0.08–0.12	0.10	0.009
	B	*M. grantii*	28	0.14–0.26	0.18	0.029
	C	*M. grantii*	100	0.09–0.24	0.15	0.070
5I length/ total length	A	*M. longifissa*	24	0.25–0.33	0.30	0.020
	B	*M. grantii*	28	0.12–0.17	0.15	0.014
	C	*M. grantii*	100	0.15–0.30	0.21	0.020

nacio, Baja California Sur. Presumably also to San Felipe, Gulf of California (Glassell 1935); commensal in the amphineuran mollusc *Cryptochiton stelleri* (Middendorff); the gastropods: *Megathura crenulata* (Sowerby), *Lithopoma undosum* (Wood) [=*Astarea undosa*], *Polinices lewisii* (Gould), *Navanax inermis* (Cooper), *Bulla gouldiana* Pilsbry, *Aplysia vaccaria* Winkler; the bivalves: *Mytilus edulis* Linnaeus, *Pholas* sp., *Tresus nuttallii* (Conrad), *Nuttalia nuttalli* (Conrad), *Zirfaea* sp., *Z. pilsbryi* Lowe, *Dinocardium robustum* (Lightfoot), *Platyodon* sp., *Modiolus* sp., *Crassedoma giganteum* (Gray), and *Macrocallista squalida* (Sowerby). Also commensal in the polychaete *Chaetopterus variopedatus* (Renier), and the holothuroids; *Parastichopus californicus* (Stimpson), *P. parvimensis* (Clark), and *Caudina arenicola* (Stimpson).

Material examined and new hosts.—3 females (1 juvenile), Punta de Sofía (27°39′N, 114°54′W), 26–27 Dec 1989, in *Pseudochama exogyra* (Conrad); 1 male, in *Modiolox capax* (Conrad); 2 males, 2 females, 28–29 Dec 1990, in *P. exogyra.* 1 juvenile female, El Rincón, in cultured *Crassostrea gigas* (Thunberg). 2 males, 3 females, La Bajada, 30–31 Dec 1990, in *Atrina tuberculosa.*

Remarks.—The occurrence of *Opisthopus transversus* in the new hosts listed above is strong evidence of the non-specificity of host for this pinnotherid (Hopkins & Scatland 1964).

Parapinnixa affinis Holmes, 1900

Parapinnixa affinis Holmes, 1900:95.—Rathbun 1918:12, 107, 111.—Glassell 1933:321–324, pl. 20, figs. 1–3, pl. 21, figs. 1–6.—Berkeley & Berkeley 1941: 54.—Schmitt et al. 1973:12, 31, 96.—Garth & Abbott 1980:614.

Distribution and host.—S.E. Siberia, S. Sachalin, Iturup, and California (type locality, Dead Man's Island, San Pedro), in tubes of the polychaetes *Terebella californica* Moore, and *Loimia montaqui* (Grube).

Material examined and new record.—1 female, La Bajada, 28 Dec 1987; intertidal, free-living, beneath rocks.

Family Bopyridae

Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1989.

Aporobopyrus sp.—Leija-Tristán & Salazar-Vallejo, 1987:179.

Pseudione sp.—Campos & Campos, 1989: 177.

Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1989:423–432, figs. 2A–G, 3A–D, table I.

Distribution and hosts.—Bahía de La Paz and vicinity, Baja California Sur, branchial parasite on *Upogebia dawsoni* Williams; and La Bajada, branchial parasites on *U. macginitieorum* Williams.

Remarks.—The present note updates both synonymy and known distribution of this species. The study of a large series of specimens including topotypes from Bahía de La Paz revealed an unrecorded morphological variation which will be discussed elsewhere (Campos & Campos, in prep.).

Family Cymothoidae
Lironeca menziesi Brusca, 1981

Lironeca n. sp.—Menzies, 1962:345.
Lironeca menziesi Brusca, 1981:173–175, figs. 15C, 19A–O.—Campos-González et al. 1986:99–104.

Distribution and hosts.—Western Baja California and the Gulf of California, including offshore Pacific Baja Islands of Coronado, Guadalupe and Alijos; parasite on the branchial chamber of *Clinocottus analis* (Girard), *Paraclinus integripinis* (Smith), and *Gobiesox maeandricus* (Girard).

Material examined and new host.—1 juvenile, Bahía Todos Santos, Baja California, 16 Oct 1989, branchial parasite of *Gobiesox rhessodon* (Smith) (Pisces: Gobiesocidae).

Remarks.—Among 10 intertidal fish species commonly inhabiting the intertidal area of Bahía Todos Santos, *Clinocottus analis* is the most infested by *Lironeca menziesi.* The preference for *C. analis* can be attributed to four exclusive features of the host: 1) it is the most abundant intertidal fish in Bahía Todos Santos area (Ruíz-Campos 1986, Ruíz-Campos & Hamman 1991); 2) it has a home behavior and also remains immobile for long periods of time (Richkus 1978); 3) it has a very expandable branchial operculum, which presumably allows the isopod's infestation; and 4) the concave operculum of the branchial chamber enables the isopod to grow more, thus increasing its fecundity. The new host *G. rhessodon,* is an inactive fish with a relative large branchial chamber. However, the relative small size and low abundance make this species less preferable for *L. mensiezi* than *C. analis.*

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REEXAMINATION OF THE MATERIAL OF *MUNIDA* LEACH (CRUSTACEA: ANOMURA: GALATHEIDAE) COLLECTED BY THE H.M.S. *CHALLENGER* (1872–1876) ALONG THE BRAZILIAN COAST

Gustavo Augusto S. de Melo-Filho and Gustavo Augusto S. de Melo

Abstract.—The material of the genus *Munida* collected by the H.M.S. *Challenger* along the Brazilian coast during its voyage of circumnavigation (1872–1876) is reexamined. Two species: *Munida sanctipauli* Henderson and *M. spinifrons* Henderson are redescribed. Part of the material of *M. stimpsoni* A. Milne Edwards collected at station 122 is in reality *M. flinti* Benedict, and specimens from the same station previously reported as *M. miles* Henderson are actually *M. forceps* A. Milne Edwards, *M. constricta* A. Milne Edwards and *M. valida* Smith. *Munida miles* and *M. stimpsoni* are not presently thought to occur off the Brazilian coast; and *M. flinti, M. forceps, M. constricta* and *M. valida* are reported for the first time from this area.

H.M.S. *Challenger* departed from Sheerness (England) on 7 December 1872, returning on 26 May 1876. During this period, on a voyage of circumnavigation, it traveled 68,890 nautical miles, establishing 362 collecting stations. The importance of this expedition was expressed by Marshall (1954): "After the world voyage of H.M.S. *Challenger,* the scientific study of the seas was given the name of Oceanography and deep-sea biology in the modern sense was firmly founded."

Among the Galatheidae of the *Challenger* collection, the genus *Munida* is prominent, with a large number of species. Although preferentially archibenthonic (Ekman 1953), this group may also be encountered in relatively shallow waters. Species of this broadly distributed genus were collected by the *Challenger* at 26 stations at depths varying from 18 to 1080 m. This material is deposited at The Natural History Museum, London (BMNH).

Along the Brazilian coast, several specimens of *Munida* were collected at Saint Paul's Rocks (St. 109, according to Saint Laurent & Macpherson 1988), Fernando de Noronha (St. 113 A), and "off Pernambuco" (St. 122). The co-ordinates 09°05′S, 34°50′W, given by Henderson (1888) for station 122 as off Pernambuco, actually correspond to Alagoas. These specimens were compared with the type material collected from the U.S. Coast Survey Steamer *Blake* (1877–1879), deposited at the Museum of Comparative Zoology, Harvard (MCZ) and the Muséum national d'Histoire naturelle, Paris (MNHN), as well as with the type material collected from the U.S. Fish Commission Steamer *Albatross* (1883), deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

The determinations made by Henderson (1888) for the specimens from station 122 (off Alagoas) were questioned by various authors (A. Milne Edwards & Bouvier 1894a, 1897; Faxon 1895; Benedict 1902; Chace 1942; Williams 1984). This material is reexamined in the present work.

The morphological description of the sternites follows the nomenclature of Zariquiey Alvarez (1952). All the specimens described, measured and figured are from the *Challenger* Expedition series.

Munida sanctipauli Henderson, 1885
Figs. 1–7

Munida sancti-pauli Henderson, 1885:411; 1888:142, pl. 3, fig. 6, 6a, b.—A. Milne Edwards & Bouvier, 1894a:256.—Benedict, 1902:251.—Chace, 1942:38.—Zariquiey Alvarez, 1952:156.—Pequegnat & Pequegnat, 1970:127.

Munida Sancti-pauli.—A. Milne Edwards & Bouvier, 1894b:85, pl. 8, figs. 11–23; 1899:74; 1900:293, pl. 6, fig. 8, pl. 29, figs. 19–21.—Bouvier, 1922:44, pl. 4, figs. 12–13.

Munida sanctipauli.—Holthuis et al., 1980: 37.—Abele & Kim, 1986:36, figs. C–D.—Saint Laurent & Macpherson, 1988:109, text-figs. 2b, d; 3b, c, e, k–o.

Munida stimpsoni.—A. Milne Edwards, 1880:47 (part.).—A. Milne Edwards & Bouvier, 1897:48 (part.).

Munida miles.—Chace, 1942:37 (part.).

Non *Munida sancti-pauli.*—Stebbing, 1902: 30; 1910:364 (=*M. benguela* Saint Laurent & Macpherson, 1988).—Barnard, 1950:489, fig. 92b (=*M. benguela* Saint Laurent & Macpherson, 1988).

Non *Munida sanctipauli.*—Kensley, 1981: 34 (=*M. benguela* Saint Laurent & Macpherson, 1988).

Material examined.—*Challenger* St. 109 (according to Saint Laurent & Macpherson 1988); 00°55′38″N, 29°22′33″W; off Saint Paul's Rocks; 29 Aug 1873; 18–108 m; 1 young male (lectotype), 1 ovig. female (paralectotype), BMNH 1888:33.

Description (based on male lectotype).—Small specimen. Carapace with slightly arched margins. Outer orbital spine on antero-lateral angle, followed by 6 strong lateral spines, decreasing gradually in size; first of these situated on posterior part of hepatic border. Gastric area with transverse row of spines on epigastric region, including 1 small pair medial to largest pair. One para-hepatic spine on each side. Anterior branchial areas each with 1 spine. Remainder of carapace unarmed. Transverse lines few, well defined, with granulose margins.

Rostrum markedly descendant. Supra-ocular spines ascendant, subparallel and long, reaching distal margin of cornea.

Eyes with corneas wider than peduncles.

Second abdominal tergite with row of 9 spines on anterior margin. Remaining tergites unarmed.

Antennular peduncle with outer terminal spine longer than inner terminal spine. Outer lateral margin with 2 spines, distal spine much longer.

Peduncle of antenna with 1 inner spine on first (basal) segment; 1 long inner spine and another short outer spine on second segment. Remaining segments unarmed.

Third maxilliped with merus bearing 2 strong spines on ventral margin, and additional tubercle between them.

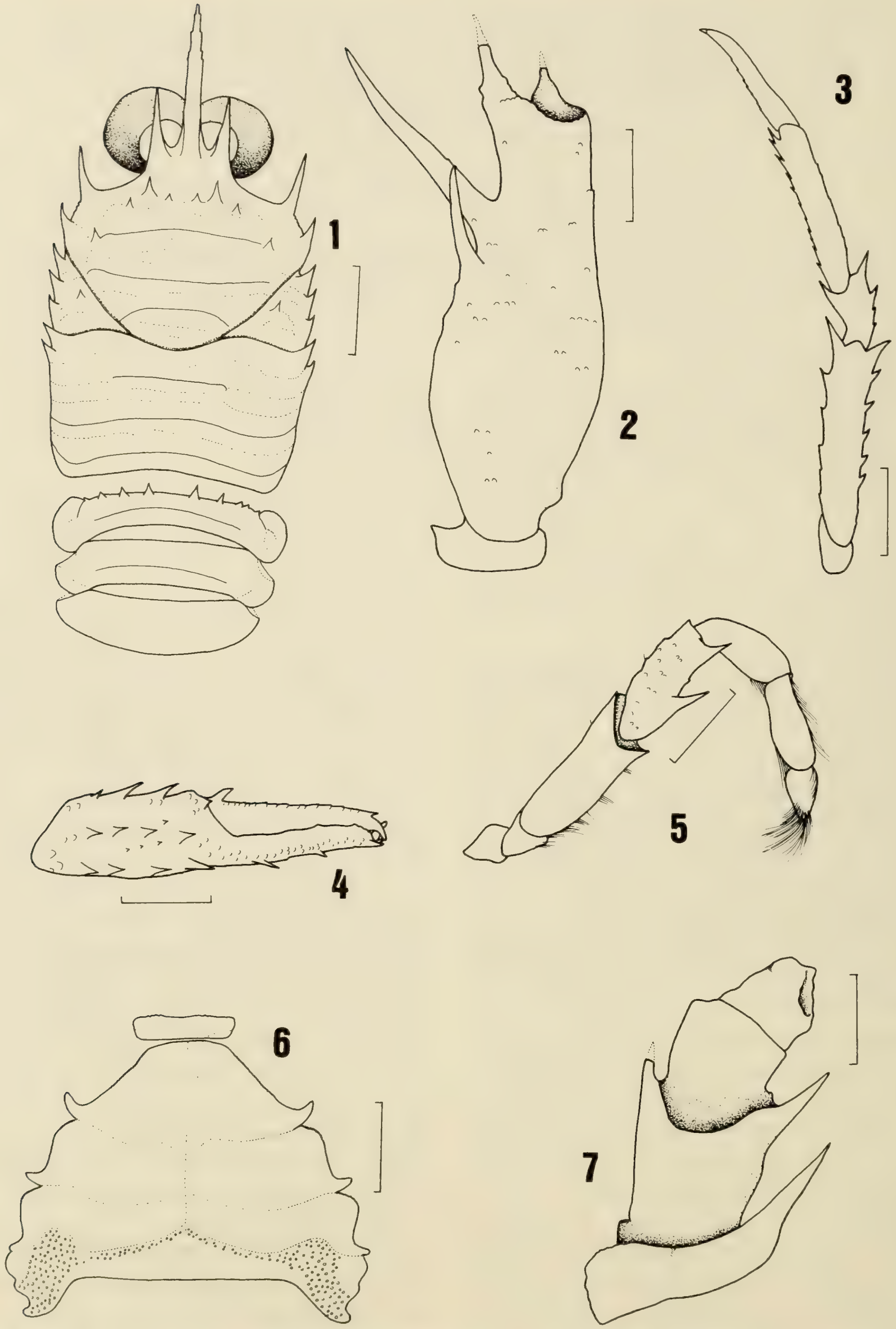
Chelipeds similar in form and size, strong, short, and spinous. Fingers without hiatus, little longer than palm.

Sternum unarmed. Sternite of third ambulatory leg strongly granulate. Sternal sulci thin, shallow, apparently naked.

Measurements in mm.—Male lectotype: Length of carapace + rostrum 10.2; carapace breadth 5.4; rostrum length 3.3; length of supra-ocular spines 1.4; cornea diameter 1.7; right cheliped: length 16.6, palm length 3.9, palm height 1.9, length of dactyl and fixed finger 4.2; left cheliped: length 16.8, palm length 3.6, palm height 1.6, length of dactyl and fixed finger 4.2.

Female paralectotype: Carapace length 9.8 (rostrum broken); carapace breadth 8.2; length of supra-ocular spines 1.7; cornea diameter 2.5; left cheliped: length 25.5, palm length 5.4, palm height 2.3, length of dactyl and fixed finger 6.2.

Distribution.—Western Atlantic: Florida, Antilles, and Brazil. Eastern Atlantic: Azores, Canaries and Moroccan coast. Commonly occurs at depths of 400–900 m;



Figs. 1–7. *Munida sanctipauli* Henderson. Lectotype male: 1, carapace and abdominal somites 2–4, dorsal view; 2, right antennular peduncle; 3, ambulatory leg; 4, right chela, dorsal view; 5, right third maxilliped; 6, sternum; 7, right antennal peduncle. Scales equal: 0.5 mm (2, 7), 1.0 mm (5, 6), 2.0 mm (1, 3, 4).

the type locality is unusually shallow (18–108 m).

Remarks.—Henderson (1888) did not specify the station number at which *M. sanctipauli* was collected, but according to Saint Laurent & Macpherson (1988), it was station 109. These authors designated as lectotype the male specimen collected at Saint Paul's Rocks; however, the specimen figured by Saint Laurent & Macpherson (figs. 2b, d; 3b, c, e, k–o) was the paralectotype ovigerous female from that same station. This specimen, besides having the rostrum broken, differs from the male lectotype by its larger size, by possessing two spines on each anterior branchial area, as well as one post-cervical spine on each side of the carapace.

Munida sanctipauli is very similar to *M. benguela* Saint Laurent & Macpherson. A good comparative study can be found in Saint Laurent & Macpherson (1988). Other similar species are: *M. constricta* A. Milne Edwards, *M. miles* Henderson, *M. valida* Smith and *M. microphthalma* A. Milne Edwards. *M. sanctipauli* differs from the first three of these species by its abdominal armature (*M. miles* with second and third tergites armed; *M. constricta* and *M. valida* with second, third and fourth tergites armed), and by the well developed form of the lateral row of spines of the carapace. Comparison of the lectotypes and paralectotypes of *M. sanctipauli* with one of the syntypes of *M. microphthalma* (*Blake* St. 35, ovig. female, MNHN Ga 960) revealed a remarkable similarity between these two species, however, the characteristically small cornea of *M. microphthalma* immediately differentiates it from *M. sanctipauli.*

The specimen collected by the *Blake* (St. 215, ovig. female, syntype of *M. stimpsoni*) determined by Chace (1942) as *M. miles,* is in reality *M. sanctipauli.*

In spite of having been first found in Brazilian waters by Henderson (1888), *M. sanctipauli* has not since been reported from this region of the Atlantic.

Munida spinifrons Henderson, 1885
Figs. 8–14

Munida spinifrons Henderson, 1885:412; 1888:144, pl. 15, figs. 1, 1a, b.—A. Milne Edwards & Bouvier, 1894a:256.—Moreira, 1901:21 and 83.—Pequegnat & Pequegnat, 1970:127.—Coelho & Ramos, 1972:171 (part.).—Abele & Kim, 1986: 36, fig. a:401.—Baba & Camp, 1988:414, fig. 1a, d–e, g, i–j, m–n.

Material examined.—*Challenger* St. 113A; 03°47′00″S, 32°24′30″W; Fernando de Noronha; 2 Sep 1873; 13–46 m; ovig. female holotype, BMNH 1888:33.

Description (based on female holotype).—Small specimen. Carapace strongly convex, with arched margins. Anterior margin strongly oblique. Outer orbital spine followed by 6 smaller spines. Epigastric row composed of 6 spines. One para-hepatic spine on each side of carapace. Anterior branchial region each with 1 spine. Remainder of carapace unarmed. Transverse lines well spaced and marked.

Rostrum long, ascendant, strongly sinuous, with distinct spines and spinules on margin. Supra-ocular spines subparallel and short, reaching only distal part of ocular peduncle. Eyes not much wider than peduncles.

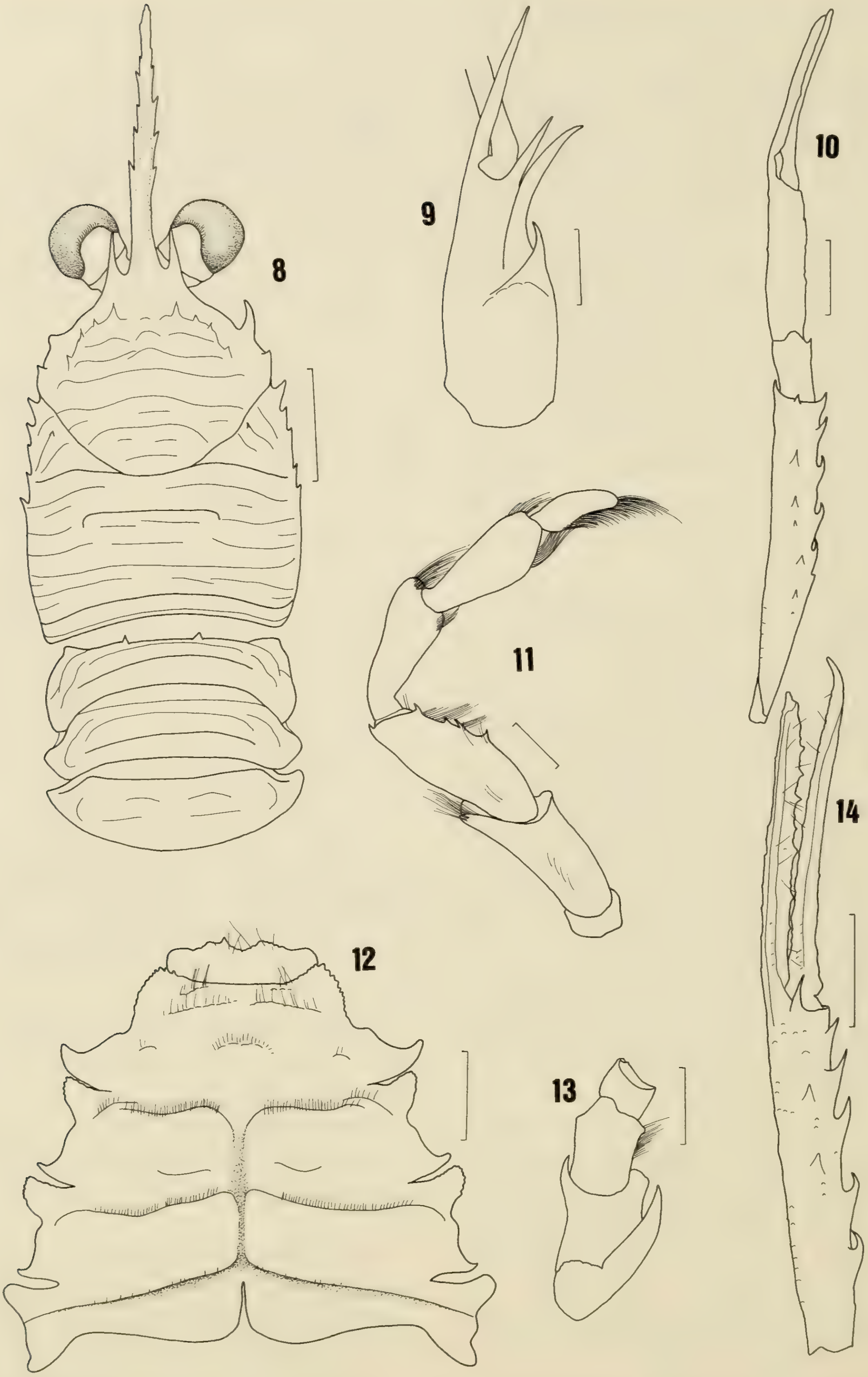
Second abdominal tergite armed with 1 pair of median spinules (0-2-0). Remaining tergites unarmed.

Antennular peduncle with inner terminal spine much longer than outer terminal spine. Outer margin with 2 spines, distal spine longer.

Antennal peduncle with inner border of first segment tapered and armed with 1 terminal spine. Second segment with 1 outer distal spine. Remaining segments unarmed.

Third maxilliped with 4 spines on ventral face and 1 terminal spine on dorsal border of merus.

Chelipeds unequal, right cheliped more robust, length of fingers similar to that of palm and with weakly developed denticles



Figs. 8–14. *Munida spinifrons* Henderson. Holotype ovigerous female: 8, carapace and abdominal somites 2–4, dorsal view; 9, left antennular peduncle; 10, left cheliped; 11, left third maxilliped; 12, sternum; 13, right antennal peduncle; 14, right cheliped. Scales equal: 0.5 mm (9, 11, 13), 1.0 mm (12), 2.0 mm (8, 10, 14).

on cutting faces. Left cheliped with fingers longer than palm, curved inward, lacking denticles on cutting face which appears only crenulate. Both chelae without hiatus.

Sternum with spinules on upper face of sternite of maxilliped and on anterior margins of sternite of cheliped. Sternal surface smooth.

Measurements in mm.—Holotype, ovig. female: length of carapace + rostrum 10.9; carapace breadth 4.9; rostrum length 4.8; length of supra-ocular spines 0.8; cornea diameter 1.4; right cheliped: palm length 6.1, length of dactyl and fixed finger 6.2, palm height 1.2; left cheliped: length 20.1, palm length 3.9, palm height 1.0, length of dactyl and fixed finger 5.3.

Distribution.—Western Atlantic: Florida and Brazil (from Ceará to Rio Grande do Norte, Fernando de Noronha and Rocas). Depth 13–91 m.

Remarks.—*Munida spinifrons* is very similar to *M. pusilla* Benedict and *M. angulata* Benedict. According to Baba & Camp (1988), *M. spinifrons* is distinguished from *M. pusilla* by having the rostrum relatively longer and with more accentuated lateral spinulation, the post-cervical spines absent, the merus of third maxilliped with 3–4 ventral spines, as well as the fingers equal to or longer than the palm. In contrast, *M. angulata* has the rostrum shorter and without lateral spinulation, besides having 1 spine on the ventral face of the antennular peduncle near the outer margin, such a spine being absent in *M. spinifrons.*

The statement of Henderson (1888) that *M. spinifrons* has 5 segments on the antennal peduncle is inaccurate. Four segments occur in species of the genus.

In spite of A. Milne Edwards & Bouvier (1897) having compared this species with *M. iris,* there is no similarity between the two.

Munida flinti Benedict, 1902
Figs. 15–16

Munida flinti Benedict, 1902:258, text-fig. 9.—Chace, 1942:57.—Pequegnat & Pequegnat, 1970:130.—Takeda & Okutani, 1983:87, text-fig. (color).

Munida Stimpsoni.—A. Milne Edwards, 1880:47 (part.).—A. Milne Edwards & Bouvier, 1897:48 (part.), pl. 4, fig. 1.

Munida stimpsoni.—Henderson, 1888:126, pl. 14, fig. 1a–b.—Moreira, 1901:21 and 83.—Coelho & Ramos, 1972:172.—Coelho, Ramos & Melo, 1989:25.

Material examined.—*Challenger* St. 122; 09°05′S, 34°50′W; off Alagoas; 10 Sep 1873; 630 m; 1 male, BMNH 1888:33. (Determined by Henderson as *M. stimpsoni.*)

Description.—Carapace with arched margins. Outer orbital spine followed by 4 small lateral spines. Gastric area with 2 pairs of spines behind supra-oculars: 1 well-developed epigastric pair, and another smaller protogastric pair. One para-hepatic spine on each side of carapace, forming hexagon with preceding spines. Anterior hepatic and branchial areas unarmed. One spine on meso-cardiac sulcus. Posterior margin of carapace with 1 pair of spines. Remainder of carapace unarmed. Transverse lines continuous, indistinct and with regularly spaced cilia.

Rostrum ascendant. Supra-ocular spines subparallel and ascendant, of medium length, reaching middle of cornea.

Eyes with corneas distinctly wider than peduncles.

Second and third abdominal tergites armed respectively with 6 (2-2-2) and 4 (1-2-1) spines on anterior margin. Fourth tergite with 2 (0-2-0) spines on anterior margin and 1 (0-1-0) on posterior margin, forming a triangle with anterior spines.

Antennular peduncle with 1 inner terminal spine little longer than outer spine. Lateral margin with 2 spines of average development. Distal part of peduncle relatively short.

Peduncle of antenna with small outer distal spine on segment 2. Remaining segments unarmed.

Third maxilliped with strong spine at middle of ventral margin.

Right cheliped long, tapered. Fingers

without hiatus, shorter than palm. Left cheliped missing.

Sternum unarmed. Anterior lateral margins of sternites crenulate. Surface of sternites adorned with crescentiform crenulations. Sternal sulci shallow, with short cilia.

Measurements in mm.—Length of carapace + rostrum 16.0; carapace breadth 10.2; rostrum length 4.8; supra-ocular spines length 2.3; cornea diameter 3.2; right cheliped: length 67.7, palm length 17.5, palm height 2.0, length of dactyl and fixed finger 12.4.

Distribution.—Western Atlantic: Gulf of Mexico, Antilles, Guianas and Brazil. Depths 108–220 m. The depth of 630 m of *Challenger* St. 122 is exceptionally great for this species.

Remarks.—The specimen collected by the *Challenger* and determined by Henderson (1888) as *M. stimpsoni* is in reality *M. flinti*; however, it differs from the holotype of the latter (USNM 9778) by having longer supra-ocular spines, more developed outer lateral spines of the antennular peduncle, and the entire sternal surface with crenulations. Nevertheless, examination of the specimens of *M. flinti* (syntypes of *M. stimpsoni*) collected by the *Blake* indicates that these characters are variable. Preliminary results of a study in progress (Melo-Filho & Melo, in prep.) of variations in *M. flinti* show that besides the characters mentioned, others commonly utilized to separate *M. flinti* from similar species, as for example the spinulation of the abdominal tergites (Pequegnat & Pequegnat 1970), are inadequate.

Munida flinti is very similar to *M. stimpsoni* A. Milne Edwards, *M. benedicti* Chace, and *M. striata* Chace, all species which apparently do not occur along the Brazilian coast. Thus, records of *M. stimpsoni* for Brazilian waters (Henderson 1888, Moreira 1901, Coelho & Ramos 1972, Coelho, Ramos & Melo 1989) actually represent variations of *M. flinti.*

Munida constricta A. Milne Edwards, 1880
Fig. 17

Munida constricta A. Milne Edwards, 1880: 52.—A. Milne Edwards & Bouvier, 1894a: 256; 1897:40, pl. 3, fig. 5.—Benedict, 1902:307.—Chace, 1942:34, text-fig. 14.—Pequegnat & Pequegnat, 1970:127.
Munida miles.—Henderson, 1888:126 (part.).—Moreira, 1901:21 and 83 (part.).

Material examined.—*Challenger* St. 122; 09°05′S, 34°50′W; off Alagoas; 10 Sep 1873; 630 m; 2 males, 1 female; BMNH 1888:33. (Determined by Henderson as *M. miles.*)

Description (based on larger male).—Carapace margins parallel. Outer orbital spine on antero-lateral angle of carapace, followed by 6 smaller spines. Gastric area with transverse row of epigastric spines, including 1 pair of small spines medially to larger pair. Two para-hepatic spines on each side of carapace. Hepatic area with few spinules. One small post-cervical spine on each side. Remainder of carapace unarmed. Transverse lines numerous, distinct.

Rostrum ascendant. Supra-ocular spines divergent and ascendant, reaching middle of cornea.

Eyes with corneas wider than peduncles.

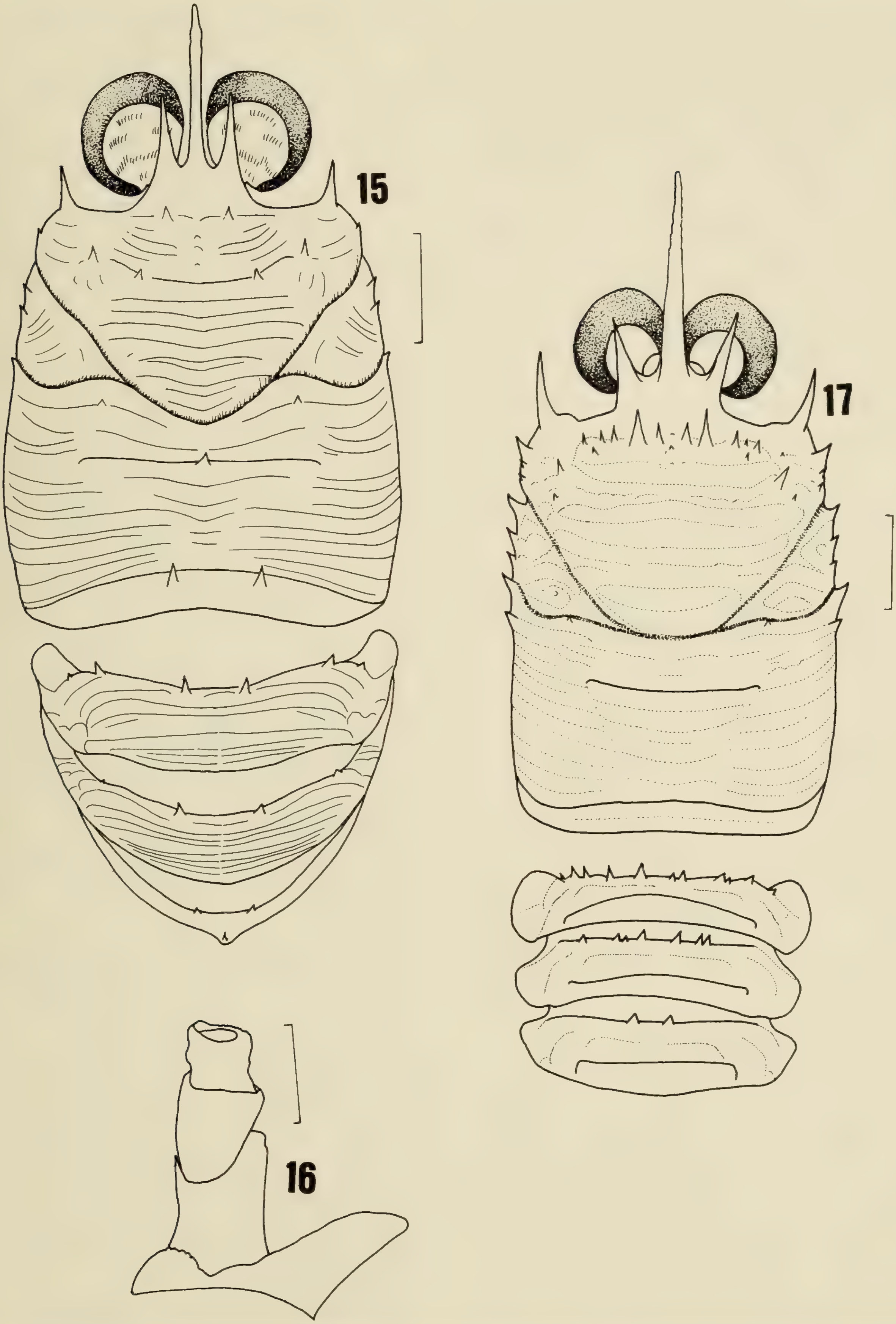
Second, third and fourth abdominal tergites armed with 11, 7 and 2 spines respectively.

Antennular peduncle with outer terminal spine slightly larger than inner terminal spine. Lateral margin with 1 long proximal spine and another very long dorsolateral spine.

Antennal peduncle with inner terminal spine on first segment (basis); second segment with 2 terminal spines, inner spine longer than outer spine.

Third maxilliped with 2 spines on ventral face of merus, distal spine smaller.

Chelipeds similar in form and size, strong, short and spinous. Chelae each with discrete proximal hiatus.



Figs. 15–17. 15–16. *Munida flinti* Benedict. Male: 15, carapace and abdominal somites 2–4, dorsal view; 16, right antennal peduncle; 17. *Munida constricta* A. Milne Edwards. Larger male: carapace and abdominal somites 2–4, dorsal view. Scales equal: 1.0 mm (16), 3.0 mm (15), 4.0 mm (17).

Sternum smooth, unarmed. Sternal sulci large, with cilia barely visible.

Measurements in mm.—Male: Length of carapace + rostrum 24.3; carapace breadth 12.0; rostrum length 7.5; supra-ocular spines length 2.3; cornea diameter 4.0; right cheliped: length 66.5, palm length 15.2, length of dactyl and fixed finger 13.2, palm height 5.9; left cheliped: length 63.5, palm length 14.9, length of dactyl and fixed finger 12.9, palm height 5.9.

Male: Length of carapace + rostrum 24.0; rostrum length 7.5; carapace breadth 11.6.

Female: Length of carapace + rostrum 18.0; rostrum length 5.9; carapace breadth 8.5.

Distribution.—Western Atlantic: Cuba, Lesser Antilles and Brazil. Depth: 227–835 m.

Remarks.—The larger male examined (24.3 mm carapace + rostrum length), has more spines on the second and third abdominal tergites than the other two specimens (a male with 10 and 2 spines, and a female with 10 and 5 spines, respectively). The female differs also by having fewer lines on the carapace and by lacking post-cervical spines and a proximal hiatus on the chela. These characteristics make the female specimen practically identical to the syntype of *M. constricta* from *Blake* St. 221 (MNHN Ga 534), which, however, has sub-parallel supra-ocular spines.

Munida constricta and *M. miles* are very similar, but, in spite of the uncertainty as to the validity of these two taxa expressed by A. Milne Edwards & Bouvier (1897:41), we are of the opinion that they are distinct. Comparison of the syntypes of both species corroborates the opinion of Chace (1942: 37) that the most important differences are in the form of the carapace (arched in *M. miles,* and with parallel margins in *M. constricta*), and in the presence of spines on the fourth abdominal tergite of *M. constricta* (invariably absent in *M. miles*).

Munida forceps A. Milne Edwards, 1880
Figs. 18–24

Munida forceps A. Milne Edwards, 1880: 49.—A. Milne Edwards & Bouvier, 1894a: 256; 1897:28, pl. 2, fig. 8.—Benedict, 1902:307.—Chace, 1942:39, text-fig. 15.—Pequegnat & Pequegnat, 1970:131, text-fig. 5-2.—Laird et al., 1976:462.—Wenner, 1982:361.—Takeda & Okutani, 1983:88, text-fig. (color).—Abele & Kim, 1986:35, fig. a:403.

Munida miles.—Henderson, 1888:126 (part.).—Moreira, 1901:21 and 83 (part.).

Material examined.—*Challenger* St. 122; 09°05′S, 34°50′W; off Alagoas; 10 Sep 1873; 630 m; 1 ovig. female; BMNH 1988:33. (Determined by Henderson as *M. miles.*)

Description.—Carapace margins slightly arched. Outer orbital spine on antero-lateral angle of carapace, followed by 5 smaller spines. Gastric area with epigastric row of strong spines. One para-hepatic spine. Anterior branchial regions each with 1 spine. One strong post-cervical spine on each side. Remainder of carapace unarmed. Transverse lines well spaced, distinct.

Rostrum ascendant. Supra-ocular spines subparallel, ascendant and short, not reaching cornea.

Eyes with cornea wider than peduncles.

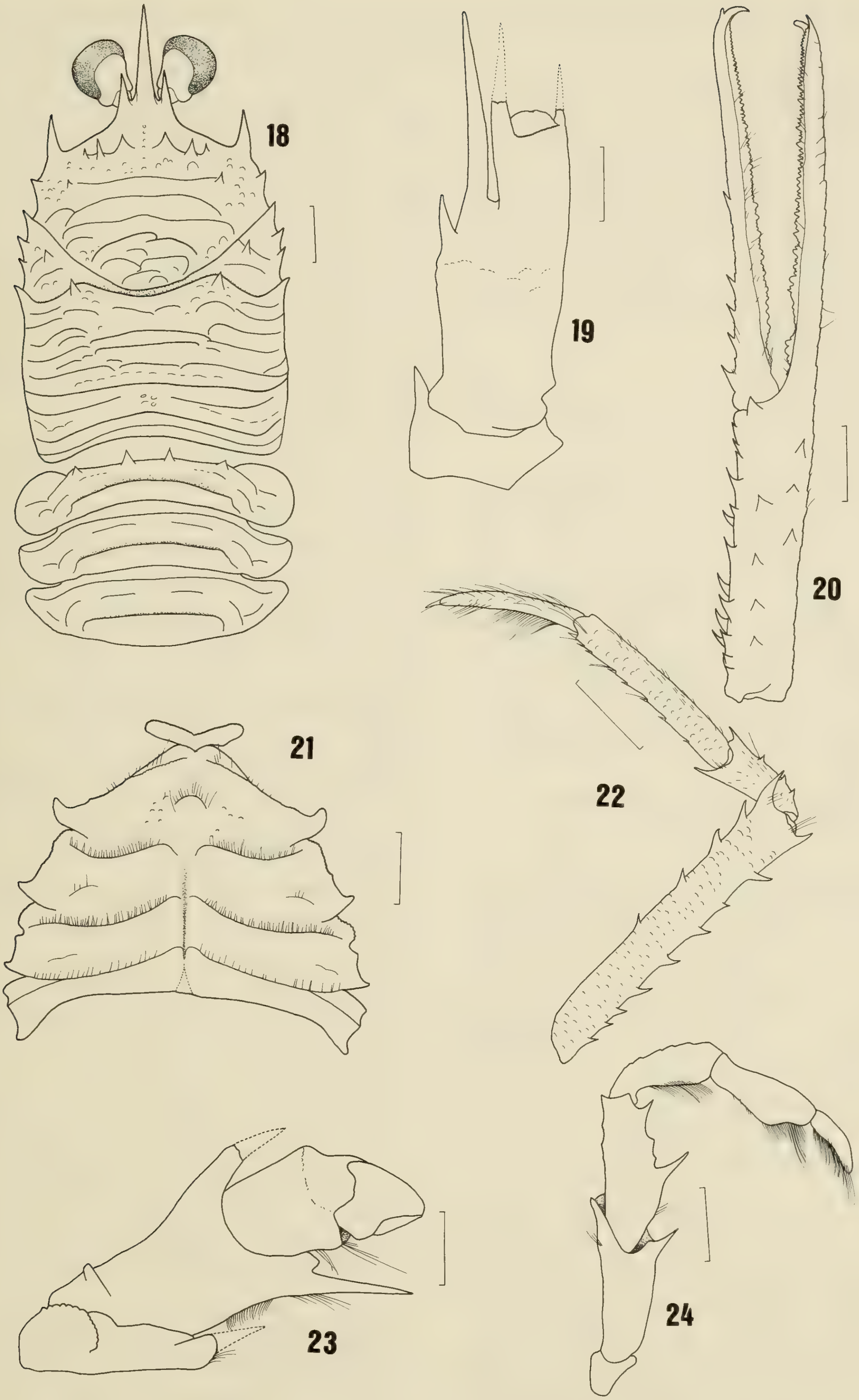
Second abdominal tergite armed with 4 spines (1-2-1); remaining tergites unarmed.

Antennular peduncle with outer terminal spine much longer than inner spine. Outer lateral margin with 1 medium-sized proximal spine and 1 very long distal spine.

Antennal peduncle with strong inner terminal spine on first segment (basis); second segment with 2 strong spines, inner spine slightly longer than outer spine; remaining segments unarmed.

Third maxilliped with 2 spines, in addition to several intercalary tubercles on ventral border of merus.

Right cheliped detached, ischium and



Figs. 18–24. *Munida forceps* A. Milne Edwards. Ovigerous female: 18, carapace and abdominal somites 2–4, dorsal view; 19, right antennular peduncle; 20, right chela, dorsal view; 21, sternum; 22, ambulatory leg; 23, right antennal peduncle; 24, right third maxilliped. Scales equal: 1.0 mm (19, 23), 2.0 mm (21, 24), 3.0 mm (18), 4.0 mm (20), 5.0 mm (22).

merus missing. Chela characteristically long and very stout.

Ambulatory legs 3 and 4 with coxae distinctly granulate.

Sternum smooth, unarmed. Sternal sulci deep medially, with dense ciliation.

Measurements in mm.—Length of carapace + rostrum 22.6; carapace breadth 14.0; rostrum length 5.1; supra-ocular spines length 1.9; cornea diameter 3.4; right cheliped: palm length 15.5, length of dactyl and fixed finger 20.2.

Distribution.—Western Atlantic: Virginia, Florida, Gulf of Mexico, Antilles, Guianas and Brazil. Depth: 80–325 m.

Remarks.—The *Challenger* specimen differs from a female reported by Chace (1942: 39, fig. 15b) in having two strong spines (instead of one) on the ventral margin of the merus of the third maxilliped. The form of the chelipeds, the somewhat small corneas, as well as the distinctly granulate coxae of the third and fourth ambulatory legs, are important characteristics of this species.

Munida valida Smith, 1883

Figs. 25–31

Munida valida Smith, 1883:42, pl. 1.—A. Milne Edwards & Bouvier, 1894a:256.—Benedict, 1902:252.—Chace, 1942:32.—Pequegnat & Pequegnat, 1970:137.—Wenner, 1982:365.—Takeda & Okutani, 1983:91, text-fig. (color).—Williams, 1984:237, text-fig. 172–173.—Abele & Kim, 1986:36, fig. e:400.

Munida miles.—Henderson, 1888:126 (part.).—Moreira, 1902:21 and 83 (part.).

Material examined.—*Challenger* St. 122; 09°05′S, 34°50′W; off Alagoas; 10 Sep 1873; 2 males and 1 female; BMNH 1888:33. (Determined by Henderson as *M. miles.*)

Description (based on smaller male).—Carapace margins subparallel. Outer orbital spine anterior to antero-lateral angle, followed by 6 smaller spines. Gastric area with 2 pairs of spines aligned with supra-oculars: epigastric pair more developed than protogastric pair. On each side of carapace, 1 barely visible spine forming hexagon with 2 preceding pairs, beside 1 para-hepatic spine aligned with protogastric pair. Anterior hepatic and branchial areas covered with tubercles and spines. One post-cervical spine on each side of carapace. Remainder of carapace unarmed. Transverse lines strongly crenulate, with numerous discontinuous lines, contrasting with some distinct continuous lines.

Rostrum descendant. Supra-ocular spines divergent, ascendant and very long, reaching past cornea.

Eyes with corneas wider than peduncles.

Second and third abdominal tergites armed with 9 and 4 spines respectively.

Antennular peduncle with outer terminal spine much longer than inner terminal spine. Lateral margin with 2 spines: 1 long proximal spine and another, even longer distal spine.

Antennal peduncle with short terminal spine on inner border of segment 1 (basis), and 2 strong terminal spines on segment 2.

Third maxilliped with 2 strong spines on ventral margin of merus, with few small tubercles between them.

Cheliped similar in form and size: strong, relatively short and spinous, with fingers lacking hiatus.

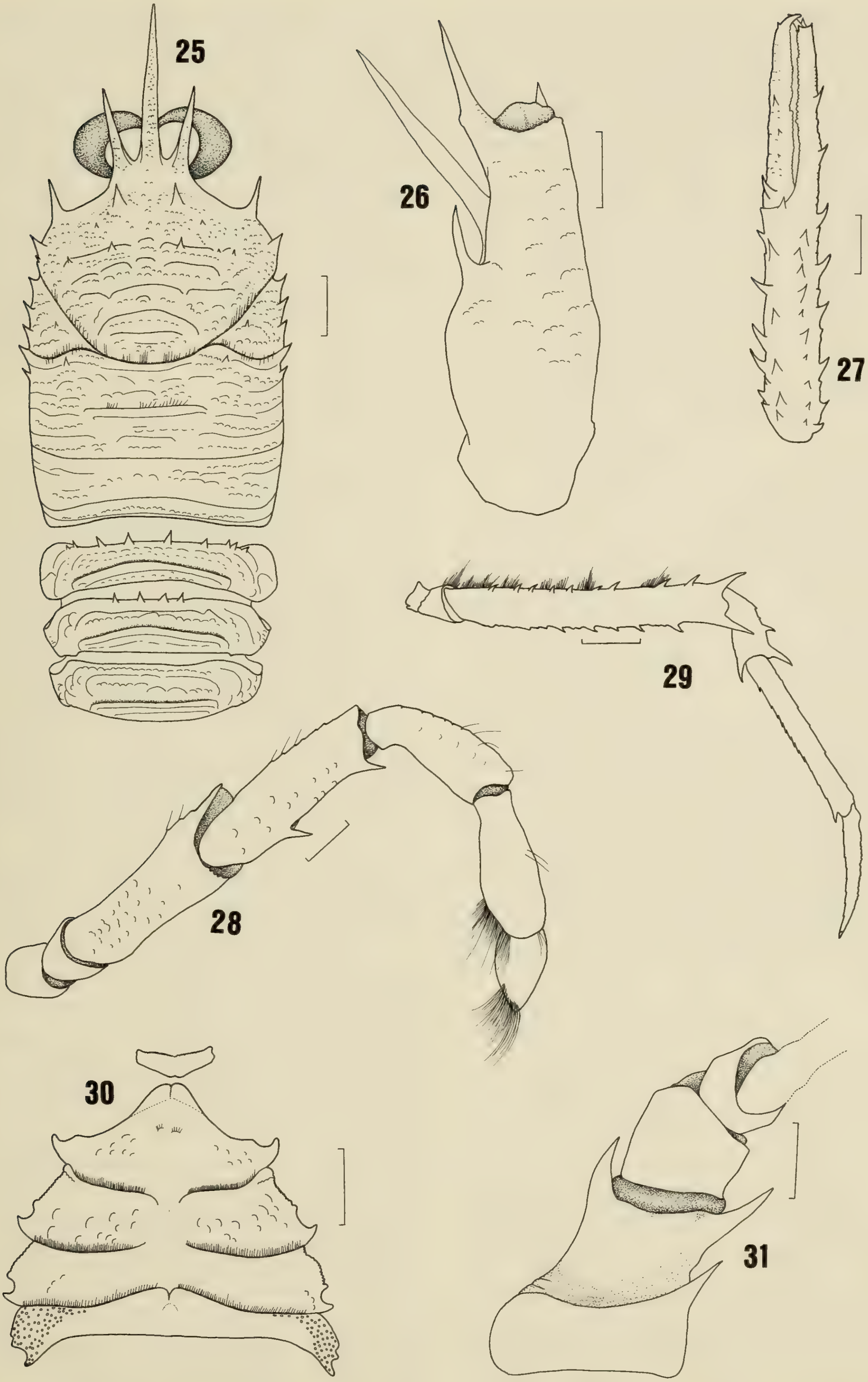
Sternum unarmed. Sternite of third ambulatory leg granulate, remaining sternites smooth. Sternal sulci wide, deep and densely ciliate.

Measurements in mm.—Male: Length of carapace + rostrum 25.1; carapace breadth 12.9; rostrum length 7.1; supra-ocular spines length 3.4; cornea diameter 3.9; right cheliped: length 51.4, palm length 12.7, length of dactyl and fixed finger 10.0, palm height 3.1.

Male: Length of carapace + rostrum 37.8; carapace breadth 19.5; rostrum length 10.5.

Female: Length of carapace + rostrum 21.2; carapace breadth 10.3; rostrum length 6.6.

Distribution.—Western Atlantic: north-



Figs. 25–31. *Munida valida* Smith. Smaller male: 25, carapace and abdominal somites 2–4, dorsal view; 26, right antennular peduncle; 27, right chela; 28, right third maxilliped; 29, ambulatory leg; 30, sternum; 31, right antennal peduncle. Scales equal: 1.0 mm (26, 28, 31), 2.0 mm (30), 3.0 mm (25, 27, 29).

eastern United States, Florida, Gulf of Mexico, Antilles, Guianas, northern South America and Brazil. Depth: 90–1823 m. According to Williams (1984), adult specimens have been collected at 0–9 m in the water column over water 384–402 m deep.

Remarks. —The larger male examined and the female differ very slightly from the specimen of *M. valida* described. These differences consist in the number of spines on the second and third abdominal tergites and in the length of supra-oculars, which do not extend past the cornea. Comparison of the *Challenger* specimens of *M. valida* with specimens of *M. miles* collected by the *Blake* (MNHN Ga 545 and 546) verified the practically unanimous opinion that these species are distinct (Benedict 1902, Chace 1942, Williams 1984). *Munida valida* is a much larger species, with longer and more divergent supra-oculars, lacking an epigastric spine row (always present in *M. miles*), and with post-cervical spines (absent in *M. miles*). In addition, the ornamentation of the carapace in *M. miles* differs in the more continuous, less distinct lines and in having a smoother surface.

Apparently *M. valida* is not morphologically very variable, an uncommon situation in the genus. All the specimens studied agree with the description of Smith (1883).

Discussion

The taxonomic complexity of the genus *Munida* derives chiefly from the high degree of morphological variation shown by many of its species (Zariquiey Alvarez 1952). This characteristic renders the dividing lines between many similar species fragile. The tendency to gregariousness and syntopy (relatively large populations of several species frequently are found in the same locality), makes it difficult to identify specimens correctly. For this reason, availability of type material is often critical. Characters fixed for a particular group of species can vary in other groups. Thus, the use of such characters in identification keys renders these keys unreliable. The older, original descriptions tend to be vague and generally based on extensive syntype series. It is therefore not surprising that Henderson mistakenly identified the numerous specimens from station 122. His opinion (Henderson 1888: 126) that *M. valida* was synonymous with *M. miles,* was certainly conditioned by the brevity of the initial description of the latter species (A. Milne Edwards 1880), which was described in detail only later by A. Milne Edwards & Bouvier (1897).

The study of the *Munida* material from the *Challenger, Blake, Albatross* and *Atlantis,* as well as abundant material collected recently off the Brazilian coast, strongly suggests the presence of four large species-complexes in the Atlantic: the *miles* complex (*Munida miles, M. benguela, M. constricta, M. forceps, M. microphthalma, M. sanctipauli* and *M. valida*); the *spinifrons* complex (*Munida spinifrons, M. angulata* and *M. pusilla*); the *stimpsoni* complex (*Munida stimpsoni, M. benedicti, M. flinti* and *M. striata*), and the *irrasa* complex (*Munida irrasa, M. iris, M. sculpta* and *M. simplex*). The latter complex is the only one not represented in the *Challenger* collections.

Reexamination of the species of *Munida* collected by the H.M.S. *Challenger* off the Brazilian coast leads us to conclude that of the four species collected in this region, two (*M. spinifrons* and *M. sanctipauli*) were described as new, and the other two were erroneously identified: *M. stimpsoni* (St. 122) was really *M. flinti,* and the material from the same station determined by Henderson as *M. miles,* in reality consists of three species: *M. constricta, M. forceps* and *M. valida.* Based on these observations we conclude that *M. stimpsoni* and *M. miles* are not known to occur off the Brazilian coast, whereas *M. flinti, M. forceps, M. constricta* and *M. valida* are cited for the first time from this area.

Acknowledgments

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PINNAXODES GIGAS, A NEW SPECIES OF PINNOTHERID CRAB FROM THE GULF OF CALIFORNIA (DECAPODA: BRACHYURA: PINNOTHERIDAE)

Timothy M. Green

Abstract.—*Pinnaxodes gigas,* new species, a large male pinnotherid from the Gulf of California is described and illustrated. Similarities with other species in the genus are discussed.

A single male specimen of a large pinnotherid was collected among sand and rocks at a depth of 20 m, off the west coast of Mexico at Morro Colorado. This species is most similar to *Pinnaxodes floridensis* Wells & Wells, 1961 and has some similarities with *P. silvestrii* Nobili, 1901 and *P. major* Ortmann, 1894. The specimen described herein is distinguished based on size, abdomen, gonopodal and third maxilliped characters. The holotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The species is illustrated.

Pinnaxodes gigas, new species
Figs. 1–3

Holotype.—Male (USNM 240150), carapace length 19.55 mm; carapace width 21.95 mm; Gulf of California, 5 miles south of Estero Tastiota, Sonora, Mexico; 28°18′45″N; 111°28′30″W; 20 m, sand and rock; collected 3 Jan 1985 by A. Kerstitch.

Diagnosis.—A large heavy bodied crab. Carapace smooth, subpentagonal, convex, front produced. Legs strong, symmetrical, in decreasing length as follows: second, third, first, fourth. Chelae strong. Propodus inflated interiorly; moveable finger with large tooth at base, immovable finger with 2 small teeth, 1 distal and 1 proximal. Abdomen broad at base, narrowing to sixth segment. Last third of sixth segment and base of telson expanded, telson narrowing to rounded tip. Third maxillipeds large, merus-ischium suture complete, outer margin nearly straight and joining broadly arched distal end, inner margin concave. Carpus broadly arched, attached at inner distal margin of merus-ischium. Propodus an elongate oval narrowing slightly distally with somewhat straight sides. Dactyl spatulate, squared distally, inserted on first third of propodus and extending just past tip of propodus. Exopod of third maxilliped with blade-like flagellum.

Description of holotype.—Carapace heavy, subpentagonal (Fig. 1). Front slightly produced, eyes just visible from dorsal view. Carapace uniformly smooth and convex, converging to steeply inclined lateral and posterolateral margins. Posterior margin narrowing somewhat, slightly convex. Edges of carapace lined with setae except for frontal region.

Buccal area broad, covered by well calcified third maxillipeds (Fig. 3A). Frontal plates and sutures dividing plates distinct. Carapace forming lateral margins of front rounded. Eyes conical. Basal segments of second antennae stout.

Third maxillipeds large (Fig. 3F). Exopod hidden by merus-ischium of endopod. Basal segment of exopod thick basally, narrowing distally; flagellum blade-like. Endopodal

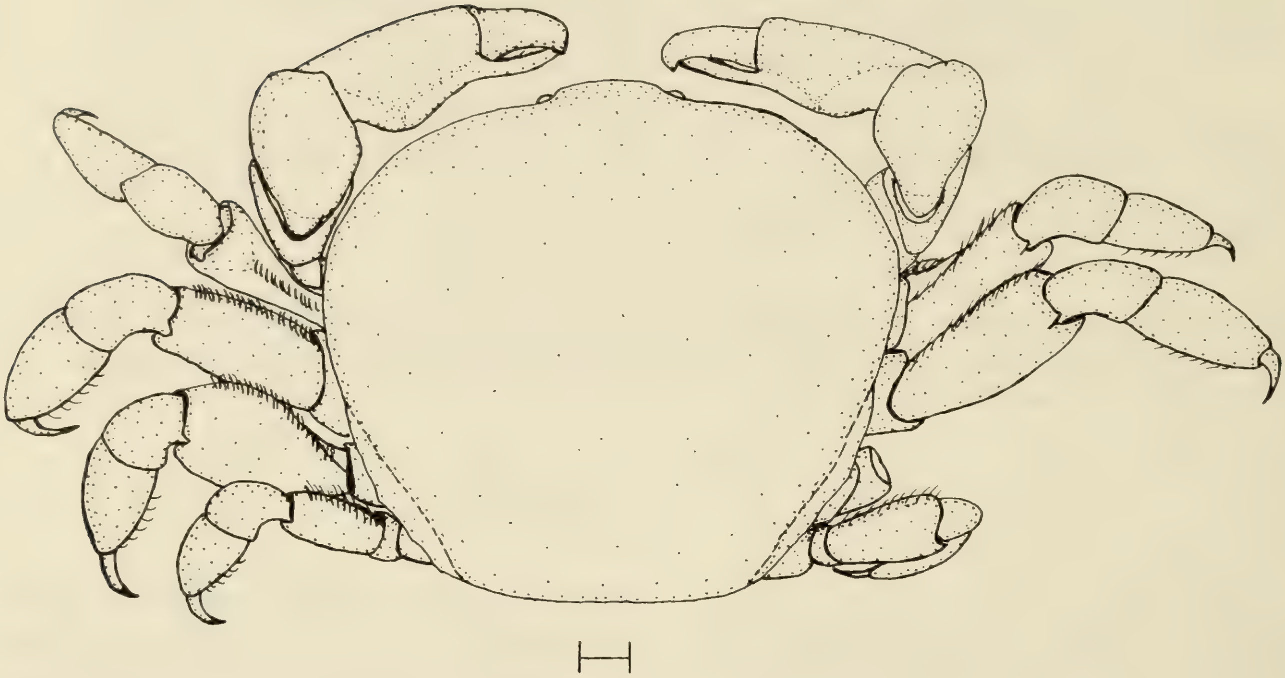

Fig. 1. *Pinnaxodes gigas,* new species. Holotype: dorsal view. Scale bar equals 2 mm.

merus-ischium suture complete. Externolateral margin nearly straight, joining broadly convexed distal margin. Inner margin concave with short depression at inner corner of merus-ischium. Carpus inflated, attached to inner distal margin of merus-ischium. Propodus an elongate oval narrowing distally with somewhat straight sides. Dactyl spatulate, distal margin squared. Dactyl inserting on first third of propodus and extending just past propodal tip. Exposed surfaces of endopod smooth, distal end of merus-ischium, carpus, propodus, and dactyl with long setae.

Chelae strong, fingers short, cylindrical, curving to sharp points (Fig. 3B). Fingers gaping over most of length, crossed at tips. Moveable finger with large tooth near base. Fixed finger with 2 small teeth, 1 distal, 1 proximal just in front of large tooth of moveable finger. Small dentition at base of fixed finger (Fig. 3D). External surface of propodus broadly convex, punctated. Internal surface inflated (Fig. 3C). Inner surface of fixed finger and propodus with line of hairs (Fig. 3D). Carpi and meri greatly expanded distally, increasing the strong appearance of chelae.

Walking legs strong (Fig. 1A), decreasing in length as follows: second, third, first, fourth. Dactyls falcate with horny tips. Meri fringed anteriorly with hairs, propodi fringed posteriorly with hairs. Ventral surfaces covered with a dense pubescence.

Thoracic sternites heavily calcified and smooth except for dense pubescence surrounding abdominal depression (Fig. 2A). Each sternite with angled lateral edge produced by posterolateral extension of sternite.

Abdomen broad basally, narrowing to telson (Fig. 2B). Distal third of sixth segment and base of telson expanded. Telson narrowing to rounded tip. Last three segments and telson with dense pubescence on margins. Proximal segments and medial portion of distal segments smooth. Tip of telson with long fringe of hairs.

Gonopods nearly as long as abdomen (Fig. 3E). Tip angled at about right angle in relation to the body of gonopods. Outer margin of gonopod flattened, inner margin angular. Outer surface with fringe of long hairs, length of angled tip with long hairs.

Coloration.—Pinnaxodes gigas is a cream colored crab with dense red-orange mottling

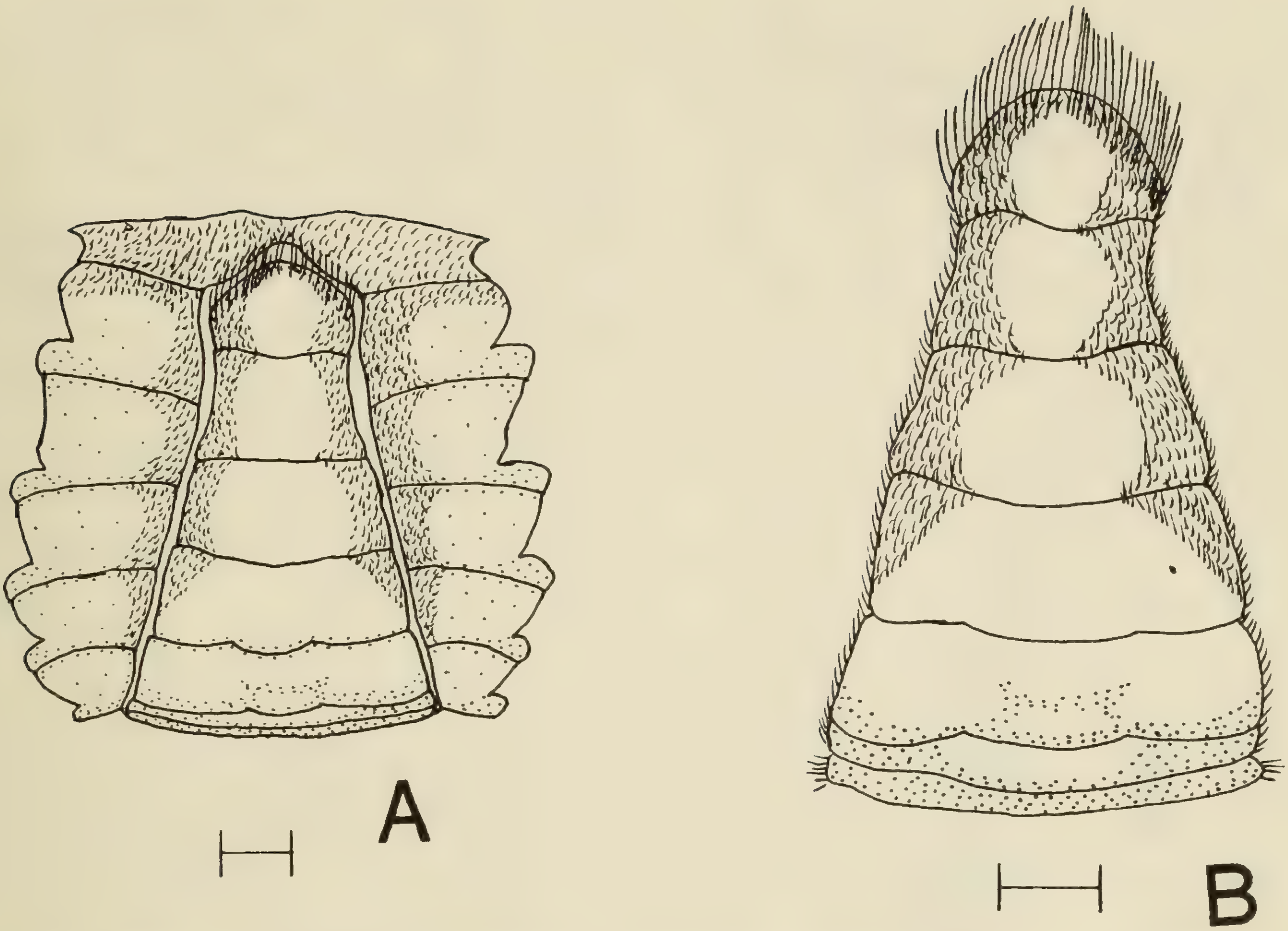

Fig. 2. *Pinnaxodes gigas,* new species. Holotype: A, sternum and abdomen, ventral view; B, male abdomen. Scale bars equal 2 mm.

in life. Mottling is found on all dorsal surfaces and dissipates when preserved, leaving only the cream colored exoskeleton.

Etymology.—The species is named for its large size; gigas is a noun in apposition.

Discussion.—A comparison of *Pinnaxodes gigas* to other species must be restricted to males and the description of the third maxillipeds of females where necessary. *Pinnaxodes gigas* is most similar to *P. floridensis* with additional similarities to *P. major* Ortmann, 1894 and *P. silvestrii* (Nobili, 1901). *Pinnaxodes gigas* is similar to these others in carapace shape, leg development and general shape of the chelae, and in the case of *P. floridensis,* coloration (Wells & Wells 1961). *Pinnaxodes gigas* can be differentiated from these species based on size, shape of abdomen, third maxillipeds, and in the case of males, the gonopods.

The size of this crab is large compared to other species of the genus, being approximately twice as large as other males. Male pinnotherids are usually smaller than females (Rathbun 1918). If females of *P. gigas* follow this general rule, then they would be larger than the 22 mm carapace width of the holotype. Females of the genus may be large (Garth 1957), often reaching the dimensions of *P. gigas.*

The shape of the abdomen is unique in that it narrows from its base to the sixth segment. The distal third of the sixth segment and the base of the telson are expanded. The telson then narrows to form a rounded tip. In *P. floridensis* the abdomen narrows to the sixth segment and has an abruptly inflated and rounded telson. *Pinnaxodes silvestrii* has a uniformly tapering abdomen joining a tapered and rounded tip.

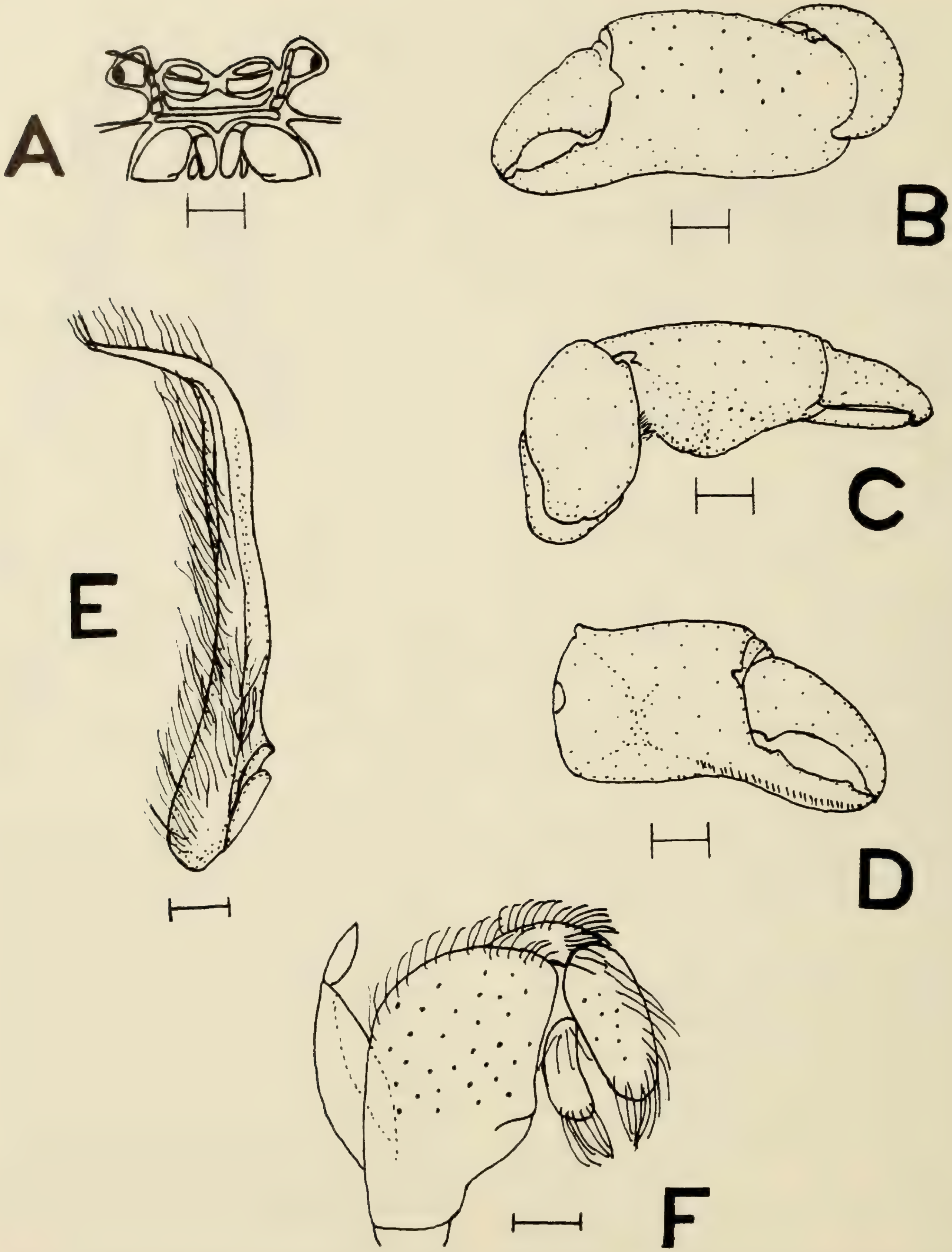

Fig. 3. *Pinnaxodes gigas,* new species. Holotype: A, front; B, left chelae, frontal view; C, left chelae, dorsal view; D, left chelae, inner view; E, right gonopod, outer view; F, right third maxilliped, outer view. Scale bars equal 2 mm, except E which equals 1 mm.

P. major has the tip of the telson flared forming a "T."

The third maxillipeds of *P. gigas* are more calcified than those of similar species. The dactyl is more angular than in the other similar species, and the propodus does not narrow toward the tip as much, being more uniform in width. The exopodal flagellum is blade-like as compared to a filiform flagellum in the other similar species.

Gonopods of *P. gigas* resemble those of *P. floridensis,* being of the same basic shape, although the gonopods of *P. gigas* are slightly more angled at the tip and the body of the gonopods are more flattened and angular.

Acknowledgments

Thanks go to A. Kerstitch who collected the crab and to Dr. M. K. Wicksten who, knowing of my interest in pinnotherids, passed it on to me.

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A NEW CRAWFISH OF THE GENUS *ORCONECTES* FROM EAST-CENTRAL MISSISSIPPI AND ADJACENT ALABAMA (CRUSTACEA: DECAPODA: CAMBARIDAE)

J. F. Fitzpatrick, Jr.

Abstract.—The crawfish *Orconectes* (*Gremicambarus*) *jonesi* is described from the Sucarnoochee River drainage in Mississippi and Alabama. Of the members of the subgenus that occur nearby, it is most closely related to *O.* (*G.*) *mississippiensis* (Faxon) and *O.* (*G.*) *chickasawae* Cooper & Hobbs. It may be distinguished from them by its wider areola, the possession of marginal rostral spines, strong cervical spines, and longer terminal elements of the first pleopod of the male.

Cooper & Hobbs (1980:1) remarked that the members of the "*virilis* section" (=subgenus *Gremicambarus* Fitzpatrick, 1987) of the genus *Orconectes* in the Mobile River basin were badly in need of clarification of identity. They further noted that because of the extreme similarity of morphology, a large series of specimens with numerous first form males is essential for correct identification of the several populations. Fortunately, a recent survey of the Sucarnoochee River drainage in east-central Mississippi and adjacent Alabama provided such a series, allowed the recognition of a distinct species therein, and provided sufficient material to permit the description that follows. Both conventional standards of length are given: total carapace length (TCL) and postorbital carapace length (POCL).

Orconectes (*Gremicambarus*) *jonesi*, new species

Fig. 1

Orconectes: Fitzpatrick & Buchanan, 1992: 65.

Diagnosis.—Body and eyes pigmented. Rostrum lacking median carina, usually with moderately thickened, slightly converging margins terminating cephalically in acute spines; distinctly acuminate. Areola 27.44 to 33.50% ($\bar{X}$ 29.86%) of total carapace length 37.09 to 44.50% ($\bar{X}$ 40.32%) of postorbital carapace length; 2.06 to 4.05 ($\bar{X}$ 3.32) times longer than wide, and with 3 to 6 punctations in narrowest part. Single cervical spine prominent; suborbital angle very weak or obsolete; branchiostegal spine small but prominent; postorbital ridges prominent and terminating cephalically in spine. Antennal scale 1.77 to 2.59 ($\bar{X}$ 2.17) times longer than wide; widest proximal to midlength. Chela depressed, mesial margin of palm with 1 or 2 rows of spiniform tubercles, latter more numerous on more mesial row; fingers only slightly gaping; males lacking tuft of setae at base of opposable margin of immovable finger, but females often with small tuft in basal ¼; mesial margin of dactyl with sparse row of subacute tubercles in basal half, if extending onto distal half then tubercles subsquamous; opposable margin of dactyl with shallow excision. Hook on ischium of third pereiopod of male; third and fourth basipodites without boss or eminence. First pleopod of first form male lacking angular shoulder on cephalic margin, rami curved throughout length, and central projection reaching nearly to cephalic margin of coxae of second pereiopods when abdomen flexed; pleopod length divisible into carapace length 2.43 to 3.58 ($\bar{X}$ 2.76) times; terminal elements slender, subparallel, but widely separated from base; central projection 24.32 to 42.67% ($\bar{X}$ 32.02%) of mesial length of pleopod, bladelike, tapering evenly to acute tip which deflected mesially to cross tip of central projection of other side, not extending so far caudally as mesial process; mesial process subcylindrical in basal ⅔ and subspatulate in distal ⅓. Annulus ventralis of female subrhomboid, wider than long, with deep trough in cephalic half overhung by high cephalomedian eminence on one side and scarcely so by another at midlength of annulus on other side; sinus originating under lesser overhang and moving nearly straight almost to caudal margin of annulus; first pleopods small, usually reaching midlength of annulus when abdomen flexed.

Holotypic male, Form I.—Eyes large and multifaceted; body pigmented; cephalothorax (Fig. 1c, f) subcylindrical in cross section; abdomen narrower than carapace (9.4 and 9.9 mm, respectively); width of latter less than depth at caudal margin of cervical groove (9.3 and 10.4 mm). Areola 29.1% of TCL (40.6% of POCL), 2.9 times longer than wide and with 4 or 5 punctations in narrowest part. Rostrum with slightly thickened elevated margins terminating in strong upturned spines; rostrum very slightly depressed, upper surface only slightly excavated; acumen prominent and slightly upturned at apex, reaching nearly to distal margin of peduncle of antenna and just beyond distal article of peduncle of antennule. Subrostral ridges weak, visible in dorsal aspect only at base of rostrum. Postorbital ridges strong, terminating cephalically in strong, laterally deflected spine. Suborbital angle nearly absent. Carapace studded dorsally with shallow setiferous punctations except in dorsal gastric region, hepatic region studded with squamous tubercles, those of left side sufficiently developed to give undulant appearance from dorsal aspect; cephalic region of branchiostegite with numerous squamous tubercles (Fig. 1c). Branchiostegal spine small but prominent. Cephalic portion of epistome (Fig. 1k) broader than long; apex markedly truncate and with tubercular thickened margin; moderately deep fovea in main body; epistomal zygoma unremarkable.

Abdomen slightly narrower than carapace (widths 10.4, 10.9 mm, respectively), and slightly longer (lengths 25.8, 24.0 mm, respectively). Pleura of second segment markedly larger than those of other segments, overlapping that of first segment and ending caudoventrally in subacute angle; pleura of third segment less angular and those of subsequent segments evenly rounded caudally. Telson with 2 acute spines in each caudolateral corner of cephalic section, mesial ones slightly movable; caudal section evenly rounded distally with hirsute margin. Basal podomere of uropods with short stout spine on distal margin of each lobe; both rami with stout median keel terminating subdistally in stout spine not overreaching caudal margin; outer ramus divided transversely by usual denticulate suture.

Antennules of usual form, basal article of peduncle with spine on ventral surface slightly distal to midlength. Antennal flagellum reaching to anterior margin of third abdominal segment. Antennal scale (Fig. 1h) 2.1 times longer than wide, with greatest width proximal to midlength; mesial margin angular; apical spine strong and reaching slightly beyond ultimate podomere of peduncle of flagellum of antenna.

Right chela (Fig. 1l) subovate in cross section, somewhat depressed. Inner margin of palm with row of 6 low spiniform tubercles (7 on left) and vaguely defined row of 5 low squamous tubercles more dorsolaterally placed; entire dorsal surface studded with setiferous punctations. Fingers slightly gaping basally; excision on movable finger shallow. Immovable finger with conspicuous median ridges above and below, dorsal one flanked by deep setiferous punctations; with

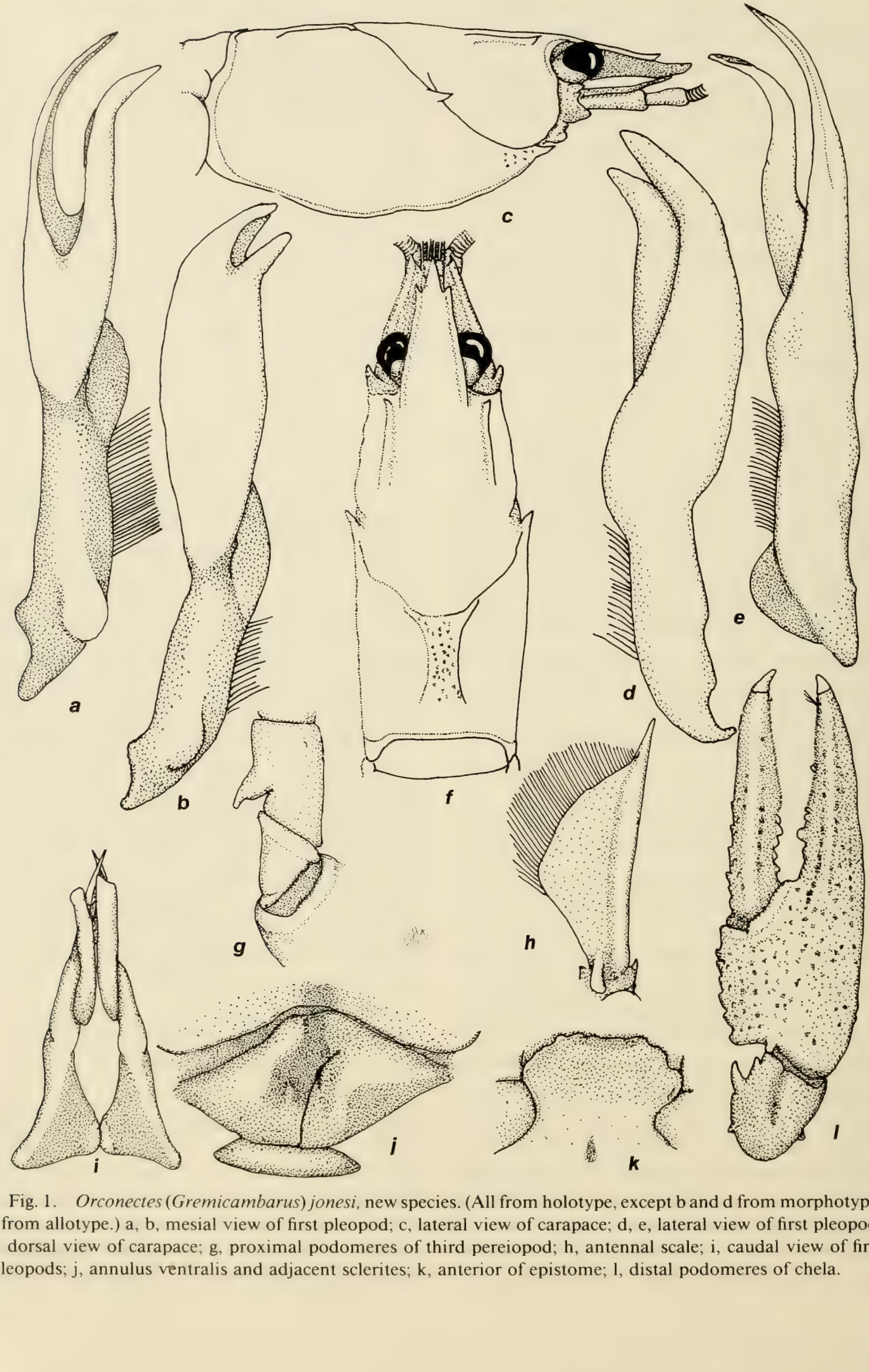

Fig. 1. *Orconectes* (*Gremicambarus*) *jonesi,* new species. (All from holotype, except b and d from morphotype, j from allotype.) a, b, mesial view of first pleopod; c, lateral view of carapace; d, e, lateral view of first pleopod; f, dorsal view of carapace; g, proximal podomeres of third pereiopod; h, antennal scale; i, caudal view of first pleopods; j, annulus ventralis and adjacent sclerites; k, anterior of epistome; l, distal podomeres of chela.

rounded costate outer margin and deep submarginal punctations in basal half; opposable margin with row of 5 prominent tubercles (third from base clearly largest) in basal half and band of crowded minute denticles in distal half; band of denticles flanked below by prominent tubercle near base of distal third of finger. Movable finger with less prominent median ridges and dorsal flanking punctations conspicuous on mesial side only; mesial margin with row of 6 spiniform tubercles in basal half, flanked dorsally by irregular row of 5 squamous tubercles; opposable margin with 5 prominent tubercles (penultimate most prominent) in basal half and band of minute denticles in distal half. Carpus about 1.4 times longer than broad, less punctate dorsally than chela, and with shallow submedian fovea in distal ⅔; mesial margin with strong spikelike tubercle flanked proximally by low, rounded tubercle (lacking on left carpus) just distal to midlength and strong rounded tubercle placed subdistally; strong spiniform tubercle in ventral mesiodistal corner and less developed tubercle in ventral laterodistal corner. Dorsal surface of merus with 2 submarginal dorsodistal acute spines; lower mesial margin with row of 9 small acute spines, distalmost strong; lower lateral margin with row of 4 strong acute spines. Ischium with single tubercle on ventromesial margin. Ischium of only third pereiopod with simple hook (Fig. 1g); hook strong and overreaching distal margin of corresponding basis but not opposed by tubercle. No prominent bosses on coxae of pereiopods.

First pleopods (Fig. 1a, e, i) symmetrical and as described in "Diagnosis," reaching coxae of second pereiopods when abdomen flexed. Apices of mesial processes distinctly truncate from caudal aspect.

Allotypic female.—Except for secondary sexual characteristics, differing from holotype in following respects: apex of rostrum reaching just to distal margin of distal article of basal peduncle of antennule; areola with only 3 or 4 punctations in narrowest part and somewhat narrower and shorter (see Table 1); distal margin of cephalic lobe of epistome more evenly rounded but still wider than long. Antennal flagellum reaching middle of third abdominal segment. Mesial margin of right chela with row of 6 spiniform tubercles and 2 low tubercles just dorsolateral to it (7 small spiniform tubercles and 3, respectively, on left); mesial margin of dactyl with 1 low spiniform tubercle followed by 2 squamous tubercles and lacking dorsolateral tubercles (all 3 tubercles low spiniform on left); inferior mesial margin of merus with row of 3 tubercles followed by 5 small spiniform ones proximal to large distal spine, inferior lateral margin with 1 distal spine (left with 10 small spiniform tubercles followed by distal spine ventromesially, and 2 distally placed spines ventrolaterally).

Annulus ventralis (Fig. 1j) fused firmly to sternum along cephalic margin, subrhom-

Table 1.—Measurements (mm) of primary types of *Orconectes* (*Gremicambarus*) *jonesi*, new species.

	Holotype	Allotype	Morphotype
Carapace			
Total length	23.0	25.0	21.7
Postorbital length	16.5	18.6	15.5
Height	10.3	11.0	9.8
Width	9.9	8.8	7.4
Areola			
Length	7.8	6.8	5.6
Width	2.3	2.6	1.6
Rostrum			
Length	8.1	8.8	7.4
Width	4.9	4.4	3.6
Chela			
Length of mesial margin of palm	5.7	4.6	4.5
Width of palm	6.5	5.0	4.5
Length of lateral margin	18.7	13.9	13.6
Length of dactyl	11.6	8.2	8.8
Abdomen			
Length	24.8	27.7	23.4
Width	9.4	12.0	7.8

boid in outline, about twice as wide as long; with deep submedian trough in cephalic half communicating with broadly ovate sulcus located in middle of annulus; right cephalolateral tubercle much elevated (ventrally) partially to overhang caudalmost part of trough and sulcus; sinus originating beneath slight median overhang of left cephalolateral tubercle nearly at midline and moving sharply caudad to traverse nearly straight line to caudal margin. Postannular plate about 3.5 times wider than long and deepest near midpoint of plate. First pleopods well developed and overlying ventral surface of annulus when abdomen flexed.

Morphotypic male, Form II.—Differing from holotype in minor respects, mostly in spiniform ornamentation of cheliped, which is more like allotype. Antennal flagellum reaching middle of third abdominal segment. First pleopod reaching only to coxae of third pereiopods; both terminal elements non-corneous, blunter and shorter than in holotype (Fig. 1b, d).

Type locality.—Pawticfaw Creek at unnumbered hard-surfaced road, 3.1 mi (5.0 km) SSE of State Route 39; T10N, R16E, sec. 27/34, Kemper County, Mississippi. The creek here was 1 m deep and up to 10 m wide; a moderately swift current flowed over a firm sand bottom that supported dense beds of *Sparganum*. The adjacent shore was dominated by stands of *Acer* and *Liquidambar*, with a conspicuous undergrowth of *Rubus*. The only other crawfish collected at this site was *Procambarus* (*Pennides*) *lagniappe* Black, 1968.

Disposition of types.—The holotypic male, Form I, the allotypic female, and the morphotypic male, Form II, are deposited in the National Museum of Natural History, Smithsonian Institution (USNM 220701, 220702, and 220703, respectively, as is a paratypic series (3 ♂I, 1 ♂II, 4 ♀, 2 ♂j, 3 ♀j). Other paratypes are located at the Museum of Natural History, University of Alabama, Tuscaloosa (UADC) (5 ♂I, 3 ♂II, 12 ♀, 5 ♂j, 9 ♀j), the Mississippi Museum of Natural Sciences, Jackson (MMNS) (3 ♂I, 4 ♂II, 6 ♀, 3 ♂j, 4 ♀j), Tulane University Museum of Natural History, Belle Chasse, Louisiana (TU) (3 ♂I, 5 ♂II, 8 ♀, 3 ♂j, 8 ♀j), and Tadashi Kawai, Ebetsu City, Hokkaido, Japan (1 ♂II, 1 ♀).

Range and material examined.—Presently the species is known only from the Sucarnoochee River drainage. Very similar forms occur in the upper reaches of the Chickasawhay and Leaf river drainages, and the tributaries of the east bank of the lower Tombigbee River are inhabited by an allied form. Until more material from these areas is available for comparison, they are tentatively assigned to this species, and the paratypes are confined to those from the Sucarnoochee (below). The Noxubee River drainage and northward are populated by *Orconectes* (*G.*) *chickasawae* Cooper & Hobbs (1980) and *O.* (*G.*) *mississippiensis* (Faxon, 1884).

Alabama—Sumter Co.: (1) Alamuchee Ck at St Rte 13, 3.8 mi (6.1 km) S of Livingston (jct. US Hwy 11), T17N, R2W, NE/4 sec 21, 1 ♀j. 22 Jun 1990, colls.: James V. Buchanan, J. F. Fitzpatrick, Jr., (UADC 147.01); (2) Alamuchee Ck at U.S. Hwy 80, 4.5 mi (7.2 km) W of Scratch Hill (jct. St Rte 17), T17N, R4W, NE/4 sec 24, 5 ♂j, 6 ♀j, 22 Jun 1990, JVB, JFF (UADC 148.01).

Mississippi—Kemper Co.: (3) type locality, 6 ♂I, 2 ♂II, 9 ♀, 2 ♂j, 3 ♀j, 26 Oct 1990, JVB, JFF (types, plus USNM 220704; UADC 150.01); (4) stream trib to Pawtickfaw Ck, 9.3 mi (15.0 km) N of Lauderdale Co. line on St Rte 39, T10N, R11E, SW/4 sec 16, 1 ♂I, 26 Jan 1990, JVB, JFF (MMNS 750); (5) Sucarnoochee Ck at Kelli's Store-Linville Rd, 1.8 mi (2.9 km) W St Rte 39, T11N, R16E, center sec 7, 1 ♂II, 27 Jan 1990, JVB, JFF (MMNS 751); (6) trib to Sucarnoochee Ck at St Rte 39, 4.7 mi (7.6 km) N of DeKalb (jct. St Rte 10), T11N, R16E, NE/4 NE/4 sec 4, 1 ♂I, 27 Jan 1990, JVB, JFF (MMNS 752); (7) trib to Sucarnoochee Ck 3.9 mi (6.3 km) S of Noxubee Co. line on St Rte 39, 0.9 mi NW on co.

rd., T12N, R16E, NW/4 sec 21, 2 ♀j, 27 Jan 1990, JVB, JFF (MMNS 753); (8) Pawtickfaw Ck at St Rte 39, 7.8 mi (12.6 km) N of Lauderdale Co. line, T10N, R16E, sec 28/29, 1 ♂II, 1 ♀, 06 Apr 1990, JVB, Lisa L. White, JFF (Kawai); (9) Creek trib to Sucarnoochee River, 7.6 mi (12.2 km) N of DeKalb (jct. St Rte 16), 0.6 mi (1.0 km) W of St Rte 39 on co. rd., T12N, R16E, NW/4 sec 21, 2 ♂II, 6 ♀, 06 Apr 1990, JVB, LLW, JFF (MMNS 754); (10) trib to Sucarnoochee Ck at St Rte 387, 9.6 mi (15.4 km) SE of Preston (jct. St Rte 21), T11N, R15E, SW/4 sec 24, 3 ♂II, 8 ♀, 06 Apr 1990, JVB, LLW, JFF (UADC 146.01); (11) trib Pawtickfaw Ck at paved road, 5.1 mi (8.2 km) E of Moscow, T10N, R15E, SW/4 sec 1, 2 ♀, 3 ♂j, 6 ♀j, 21 Jun 1990, JVB, JFF (TU 6440); (12) Sucarnoochee R at St Rte 16, 3.2 mi (5.1 km) E of DeKalb (jct. St Rte 39), T11N, R17E, SW/4 sec 19, 1 ♀j, 23 Jun 1990, JVB, JFF (MMNS 756); (13) trib Pawtickfaw Ck at US Hwy 45, 4.7 mi (7.6 km) N of Lauderdale Co. line, 0.2 mi (0.1 km) W on dirt rd, T9N, R18E, SW/4 sec 7, 1 ♀j, 07 Jun 1990, J. M. Boyle, JVB (MMNS 757); (14) Straight Ck at hard-surfaced rd, 6.1 mi (9.8 km) W of US Hwy 45, T10N, R17E, sec 9/16, 3 ♂I, 26 Oct 1990, JVB, JFF (UADC 149.01); Lauderdale Co.: (15) Big Reed Ck at US Hwy 45, 15.3 mi (24.6 km) N jct US Hwy I20/I59, 1.9 mi (3.1 km) S of Kemper Co. line, T8N, R17E, NE/4 NE/4 sec 12, 4 ♂II, 4 ♀, 04 Apr 1990, JVB, JFF (TU 6439); 3 ♂I, 1 ♂II, 2 ♀, 2 ♀j, 27 Oct 1990, JVB, JFF (TU 6441); (16) Ponta Ck at St Rte 39, 12.2 mi (19.6 km) N of Meridian (jct. US Hwy I20/I59), T8N, R16E, NE/4 sec 21, 1 ♂j, 22 Jun 1990, JVB, JFF (MMNS 755); (17) Ponta Ck, 2.1 mi (3.4 km) ESE of entrance to Meridian Naval Air Station on hard-surface rd, T8N, R17E, SW/4 NW/4 sec 22, 1 ♂I, 1 ♂II, 2 ♀, 27 Oct 1990, JVB, JFF (MMNS 758).

Variations.—Most of the variation seen was in the nature and development of the various spinose and tubercular ornamentation, especially of the chelipeds. The mesial margin of the palm had from one to seven spiniform tubercles, the most common number being five (35% of specimens examined) followed closely by six and four; the more dorsal row of squamous tubercles varied from zero to seven, with zero and two being subequal in frequency (22% of specimens); four first form males and one female exhibited tubercles below the mesialmost row, the maximum (in two animals) being three. Comparable variation in the tubercular ornamentation of the dactyl occurred. The merus likewise varied in the number of spines along the lower surfaces: lateral one to four and mesial two to 11. The number of punctations in the narrowest part of the areola were 3–4 (13.5% of specimens), 4–5 (29.7%), 5–6 (45.9%), or 6–7 (10.9%); these figures are markedly greater than those for *O. chickasawae.*

Next most variable was the epistome. The cephalic margin frequently was broadly rounded, and almost as often broadly truncate; the ratio of length to width, however, remained near 1.2.

I did not encounter a single female in which the annulus was the reverse image of the allotype, although dextral variations probably exist. And as one can expect, juvenile specimens often were devoid of the spines or tubercles on the chelipeds that distinguish adult specimens.

Size.—The largest animal, a first form male, was taken 27 Jan 1990 from a tributary to Sucarnoochee Creek, 4.7 mi (7.6 km) south of DeKalb on St. Rte. 39, and it measured 29.2 mm TCL (POCL 21.2 mm); the smallest Form I male was 18.5 mm TCL (POCL 13.6 mm). The largest second form male and female were 29.0 (POCL 21.3) and 30.0 (POCL 22.6) mm, respectively. There was no apparent correlation of size with any portion of the drainage.

Based on the type series, *O. jonesi* seems to be somewhat smaller than either *O. chickasawae* or *O. mississippiensis* (see size reports in Cooper & Hobbs, 1980:34, 41).

Life history notes.—The breeding period seems to begin in what, for the latitude, is early fall (October), with ovigerous females appearing in late winter (January). In October, 1990, the male : female ratio was 1.42, and 76% of the males were Form I. By January, the dominance of Form I males persisted, but female numbers fell sharply. This would be consistent with ovigerous females being more secretive and thus less likely to be in open water, a phenomenon documented for other species of crawfishes. By summer, juveniles dominate the populations, but by fall their numbers decline to about 20%, a status they maintain throughout the winter. These probably represent a reserve breeding stock in the event that the usual reproductive season should fail. These possibilities were dramatized just before the study period, when torrential rains in late 1989 were very destructive to the habitat and the summer of 1990 was unusually dry in the local geographic area.

Relationships.—*Orconectes* (*Gremicambarus*) *jonesi* is a member of the species complex allied to *O.* (*G.*) *chickasawae* and *O.* (*G.*) *mississippiensis* (Faxon, 1884). These were discussed at some length by Cooper & Hobbs (1980:34–35), so that here it seems adequate to distinguish *O. jonesi* only from its geographically proximate relatives. In *O. mississippiensis* the areola is obliterated for at least a part of its length. Although open, the areola of *O. chickasawae* has room for at most one punctation in its narrowest part. In contrast, *O. jonesi* has a minimum of three punctations in this area, which is markedly wider (*O. chickasawae* is at least 16 times longer than wide, compared with a maximum value of 4.05 in *O. jonesi*). Quite significant is the relative length of the central projection (the "split" of the pleopod of the writers of a century ago). In *O. jonesi* Form I males this value averages 32.02% of the total length of the appendage, whereas in *O. chickasawae* it averages 21.9% with a maximum length of 26.4%, scarcely overlapping the minimum length (24.3%) of *O. jonesi.* In length of the central projection, *O. jonesi* more closely approaches *O. mississippiensis* (31.5–35.6% of pleopod length), but the open areola, length of rostral marginal spines, and a less sharply recurved apex of the central projection will serve to distinguish *O. jonesi* from the latter species. In many respects, *O. jonesi* is more like *O.* (*G.*) *etnieri* Bouchard and Bouchard (1976), but the latter species has a sharply recurved apex of the central projection and is apparently confined to tributaries of the east bank of the central portion of the Mississippi River.

Numerous populations of similar *Orconectes* occur in the Yazoo and Big Black drainages in Mississippi. There are inadequate series, especially of first form males, to allow determinations of the realtionships of these to *O. etnieri* and *O. jonesi.* Also the upper Chickasawhay and upper Leaf river basins, as well as tributaries of the central east-bank Tombigbee watershed, are occupied by populations of *Orconectes* closely allied to *O. jonesi* and *O. chickasawae.* Again, they are not adequately represented in collections to permit speculation concerning their position in this complex of *Gremicambarus* species.

The differences in habitat requirements for *O. chickasawae, O.* (*G.*) *holti* Cooper & Hobbs (1980), *O. mississippiensis,* and *O. jonesi* are striking. The former three species seem to prefer sluggish to moderately flowing streams, sometimes occurring in ditches. On only two occasions (at localities 11 and 16 under "Range") were adult *O. jonesi* collected from other than moderately to swiftly flowing waters; never was it encountered in a ditch. Indeed, usually *O. jonesi* dominated the riffle areas and *Sparganum* beds where it occurred.

Crawfish associates.—In the Sucarnoochee basin the following species were from habitats containing *O. jonesi*: *Cambarus* (*Depressicambarus*) *striatus* Hay, 1902, *C.* (*Lacunicambarus*) *ludovicianus* Faxon, 1884, *Procambarus* (*Ortmannicus*) *acutissimus* (Girard, 1852), *P.* (*O.*) *acutus* (Girard, 1852), and *P.* (*Pennides*) *lagniappe.* In one instance (at locality 12, above), a juvenile assignable to *Gremicambarus* was collected; it has an obliterated areola and thus is tentatively assigned to *O. mississippiensis,* but it is the only record of the species from south of the Noxubee River drainage.

Etymology.—It pleases me to be able to name this species in honor of Robert L. Jones, Curator of Invertebrates at the Mississippi Museum of Natural Science and formerly biologist with the Mississippi Natural Heritage Program. His strenuous efforts in the field have contributed much to our knowledge of Mississippi crawfishes.

Acknowledgments

Thanks are due to Mr. James V. Buchanan, Mr. James M. Boyle, and Ms. Lisa L. White, all of the University of South Alabama, for assistance in the field. Dr. Horton H. Hobbs, Jr. of the Smithsonian Institution offered many helpful criticisms of the manuscript. Without financial support from the "checkoff" funds allocated by the Mississippi Natural Heritage Program for a study of *P. lagniappe,* this study would not have been possible.

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THE FRESHWATER CRABS AND PALAEMONID PRAWNS (CRUSTACEA: DECAPODA) OF BATAM ISLAND, RIAU ARCHIPELAGO, INDONESIA, INCLUDING DESCRIPTIONS OF TWO NEW SPECIES

Peter K. L. Ng

Abstract.—The freshwater crab (Brachyura: Parathelphusidae) and prawn (Caridea: Palaemonidae) fauna of the island of Batam in the Riau Archipelago, Indonesia, is documented and discussed. Three species of crabs *Parathelphusa maculata* De Man, 1879, *Parathelphusa batamensis,* new species, and *Irmengardia nemestrinus,* new species, and two species of prawns, *Macrobrachium malayanum* (Roux, 1936) and *Macrobrachium trompii* (De Man, 1898) are recorded. Descriptions and figures are provided for the two new brachyuran taxa.

In a recent survey of the aquatic fauna in the forests of Batam, a large island some 20 km southeast of Singapore, in the Riau Archipelago (Fig. 1), numerous specimens of brachyuran crabs and prawns were obtained. The island of Batam, which covers some 400 km^2, is being rapidly developed, and large tracts of land are currently being or already have been cleared for housing, industrial and commercial projects. The scale of the development plans are such that much of the native freshwater fauna will be (if not already) under serious threat in the years to come. As almost nothing is known about the freshwater decapod fauna of Batam, a brief account of the species present will thus be of interest.

A total of three brachyuran species of the family Parathelphusidae, *Parathelphusa maculata* De Man, 1879, *Parathelphusa batamensis,* new species, and *Irmengardia nemestrinus,* new species, and two caridean prawns of the family Palaemonidae, *Macrobrachium malayanum* (Roux, 1936) and *Macrobrachium trompii* (De Man, 1898) were collected. A brief account of these species, including descriptions and remarks on the two new taxa, is presented in this paper.

Measurements for the crabs are listed as carapace width by carapace length. The terminology used follows that by Ng (1988). The abbreviations cl, rl and bl are for the prawn carapace, rostral and body lengths respectively. The carapace length is measured from the postorbital margin to the posterior margin of the carapace; rostral length from the tip of the rostrum to the postorbital margin; and the body length from the tip of the rostrum to the posterior margin of the telson. Specimens are deposited in the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore. The collecting sites are indicated on Fig. 1 and correspond to the site numbers in the materials examined for each species.

Systematic Account

Family Parathelphusidae

Parathelphusa maculata De Man, 1879

Material examined.—3 males (largest 30.0 by 23.5 mm), 2 females (28.1 by 22.3 mm), ZRC, sites 2, 3, 4, southwestern and eastern Batam island, leg. P. K. L. Ng, 21 Jan 1992.

Remarks.—This common lowland species is known from southern Sumatra, Peninsular Malaysia and Singapore (see Ng

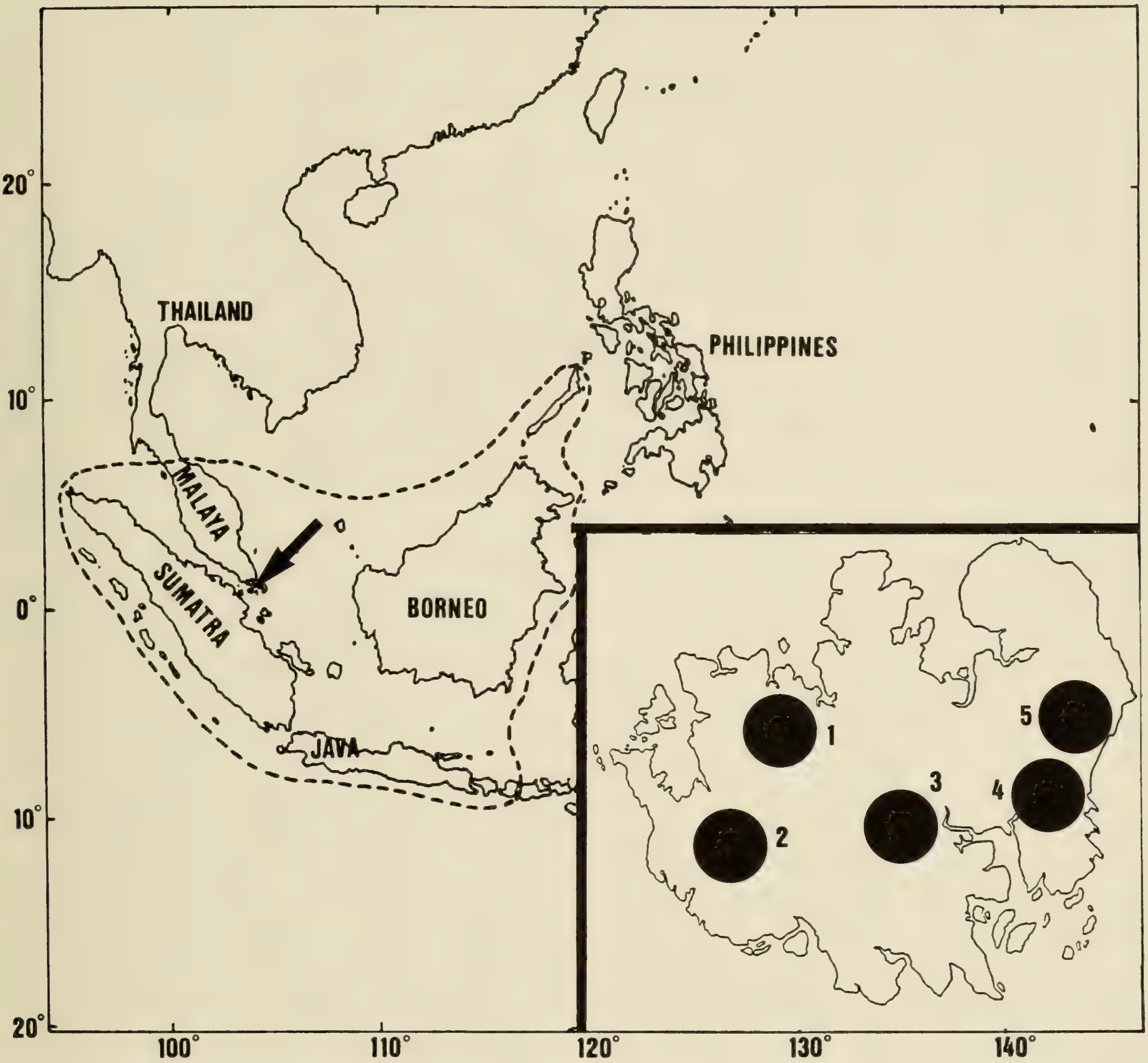

Fig. 1. Map of Southeast Asia, showing the position of Batam island (arrow) in the Riau Archipelago, Indonesia. The dashed lines demarcate the Sunda Shelf. Inset: Map of Batam, Riau Archipelago, showing collecting sites.

1988, 1990b). (See *Remarks* for next species.)

Parathelphusa batamensis, new species
Fig. 2

Material examined.—Holotype male (29.6 by 24.2 mm), ZRC, 7 paratype males, 4 paratype females (largest 28.7 by 23.0 mm), ZRC, site 1, peat swamp forest streams, fringed by *Pandanus,* western Batam island, Riau Archipelago, Indonesia, leg. P. K. L. Ng & K. K. P. Lim, Feb 1991.

Description.—Carapace transverse, gastric and branchial regions slightly swollen, surfaces smooth, evenly convex, with numerous black spots, especially on lower half of body, pterygostomial, sub-branchial and suborbital regions. Frontal margin straight, frontal median triangle well formed; external orbital angle truncate, outer margin convex to sinuous, anterolateral margin with 2 epibranchial teeth, teeth directed forwards, posterolateral regions with strong oblique striae. Epigastric and postorbital cristae

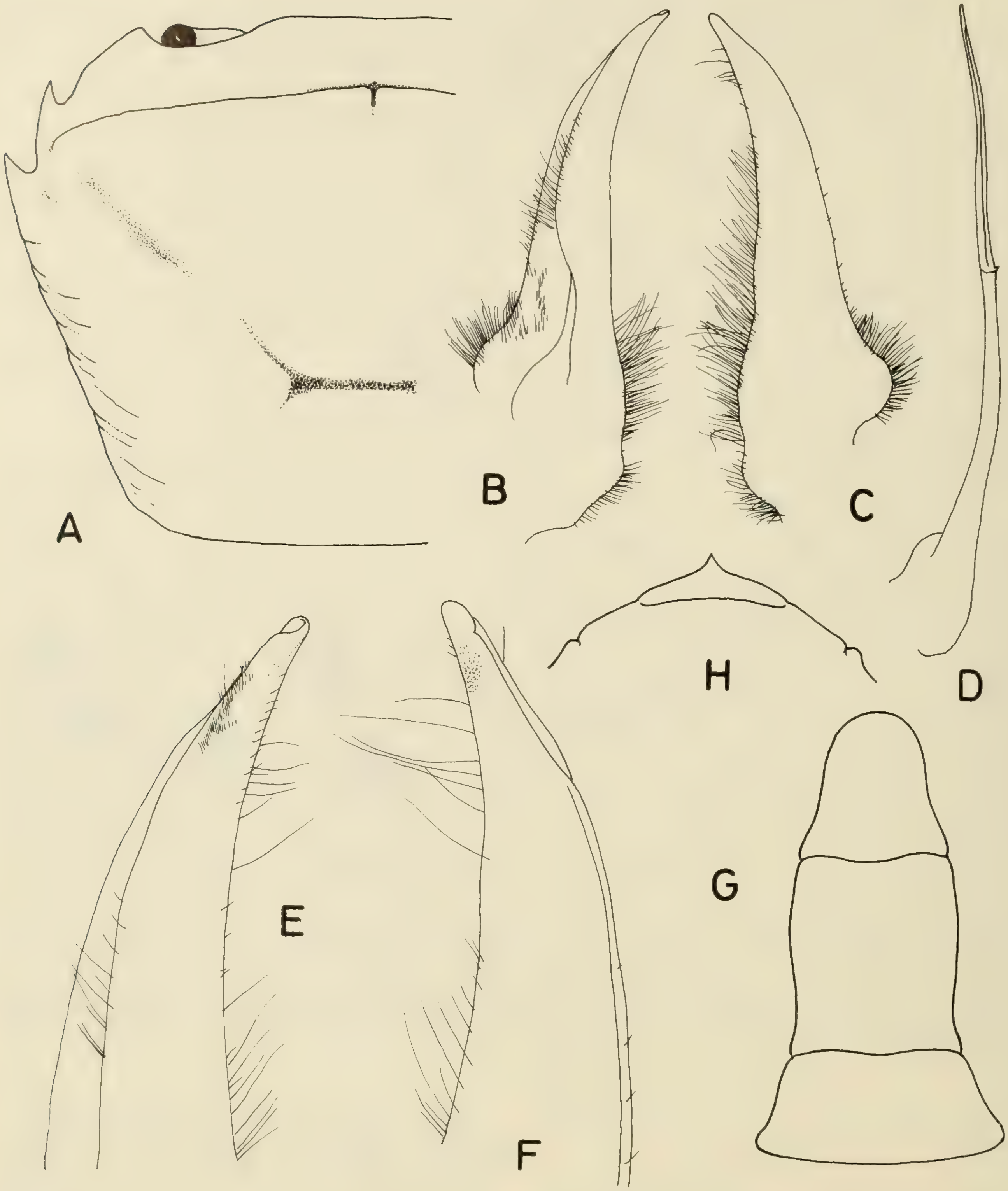

Fig. 2. *Parathelphusa batamensis*, new species. Holotype, 29.6 by 24.2 mm, ZRC, Batam. A, left side of carapace; B, C, E, F, left G1s; D, left G2; G, last three abdominal segments; H, anterior part of sternum. (B, E, ventral views; C, F, dorsal views; E, F, distal part of G1)

sharp, strong, confluent, subparallel to frontal margin, external edges stopping just before base of first epibranchial tooth, epigastric cristae separated by deep cleft. Cervical grooves shallow; H-shaped central depression deep, prominent. Third maxilliped exopod with long flagellum on exopod.

Chelipeds subequal in males; outer surfaces smooth, black spots present on upper half of palm and dactylus; fingers longer than palm in both sexes, not pigmented black, distal part beige-colored. Carpus with well developed sharp spine and basal denticle on inner distal margin; merus with sharp subdistal spine on upper margin.

Second ambulatory leg longest, with distinct sharp subterminal spine on each of the dorsal meral margins of first 3 pairs, merus of last pair with blunt subdistal knob.

Suture between sternal segments 2 and 3 slightly concave towards buccal cavity, with distinct marginal notch between segments 3 and 4. Male abdomen T-shaped, lower margin of segment 4 slightly convex in adults; segment 7 distinctly longer than half length of segment 6.

G1 stout, gently bent outwards, outer margin of proximal part of subterminal segment entire, not clefted at proximal part, tip rounded. G2 with long distal segment, about 0.69 times length of basal segment.

Etymology.—The new species is named after its island of origin, Batam.

Remarks.—*Parathelphusa batamensis,* new species, belongs to the same group of species as *P. maindroni* (Rathbun, 1902) (see Ng 1992). Its carapace is swollen, but not to the degree of *P. maindroni, P. reticulata* Ng, 1990a, or *P. convexa* De Man, 1879. In its carapace physiognomy, *P. batamensis* is closest to *Parathelphusa oxygona* Nobili, 1903 (incorrectly synonymized with *P. incerta* (Lanchester, 1900), by Bott 1970, see also Ng 1990b), but differs in the form of the external orbital angle (outer margin distinctly sinuous but straight in *P. oxygona*) and the outer edge of the postorbital crista reaching the median part of the base of the first epibranchial tooth (reaches between the base of the first epibranchial tooth and external orbital angle in *P. oxygona*). The G1 of *P. batamensis* is very different from that of *P. oxygona* in having the distal part more strongly curved, the tip being directed laterally outwards (straighter, the tip directed upwards in *P. oxygona*). The carapace patterns of live or fresh specimens of both species are quite different. In *P. batamensis,* the carapace is distinctly spotted, the background color being dull orange. In *P. oxygona,* the spots are smaller, more diffuse, forming rosette-like patterns.

Ecology.—All the specimens of *P. batamensis* were obtained from one area on the western part of the island, with the forests there being intermediate between freshwater and peat swamps (sensu Anderson 1964). They were collected from a well shaded, shallow, relatively fast flowing blackwater stream in a disturbed swamp forest. The banks were overgrown with *Pandanus,* and the waters were dark tea-colored. The pH of the water was about 5. The substrate was clay and leaf detritus. The crabs were obtained from burrows along the waterline as well as among the submerged roots and leaf litter. On the southern and eastern parts of the island where typical freshwater swamps are present, only *P. maculata* was present instead. The situation here seems to parallel that in Singapore, where in typical forest habitats, *P. maculata* is found, whereas in the more acidic waters deeper in the swamp forests, it is replaced by *P. reticulata* instead (see Ng 1990a, 1990c). The carapace of the two species are similar, although that of *P. batamensis* is more punctated and the gastric regions slightly more inflated. The G1s of all the males of both species (including young specimens) were examined, and they are consistent for each species as currently defined.

Irmengardia nemestrinus, new species

Fig. 3

Material examined.—Holotype male (16.9 by 14.5 mm), ZRC, 5 paratype males, 1 paratype female, 2 paratype juveniles, ZRC, site 3, northeastern Batam island, leg. P. K. L. Ng et al., 29 Jan 1992.

Description.—Carapace squarish, high, surfaces smooth, dorsal surface with scattered and indistinct black spots. Frontal margin almost straight, with well developed frontal median triangle; external orbital an-

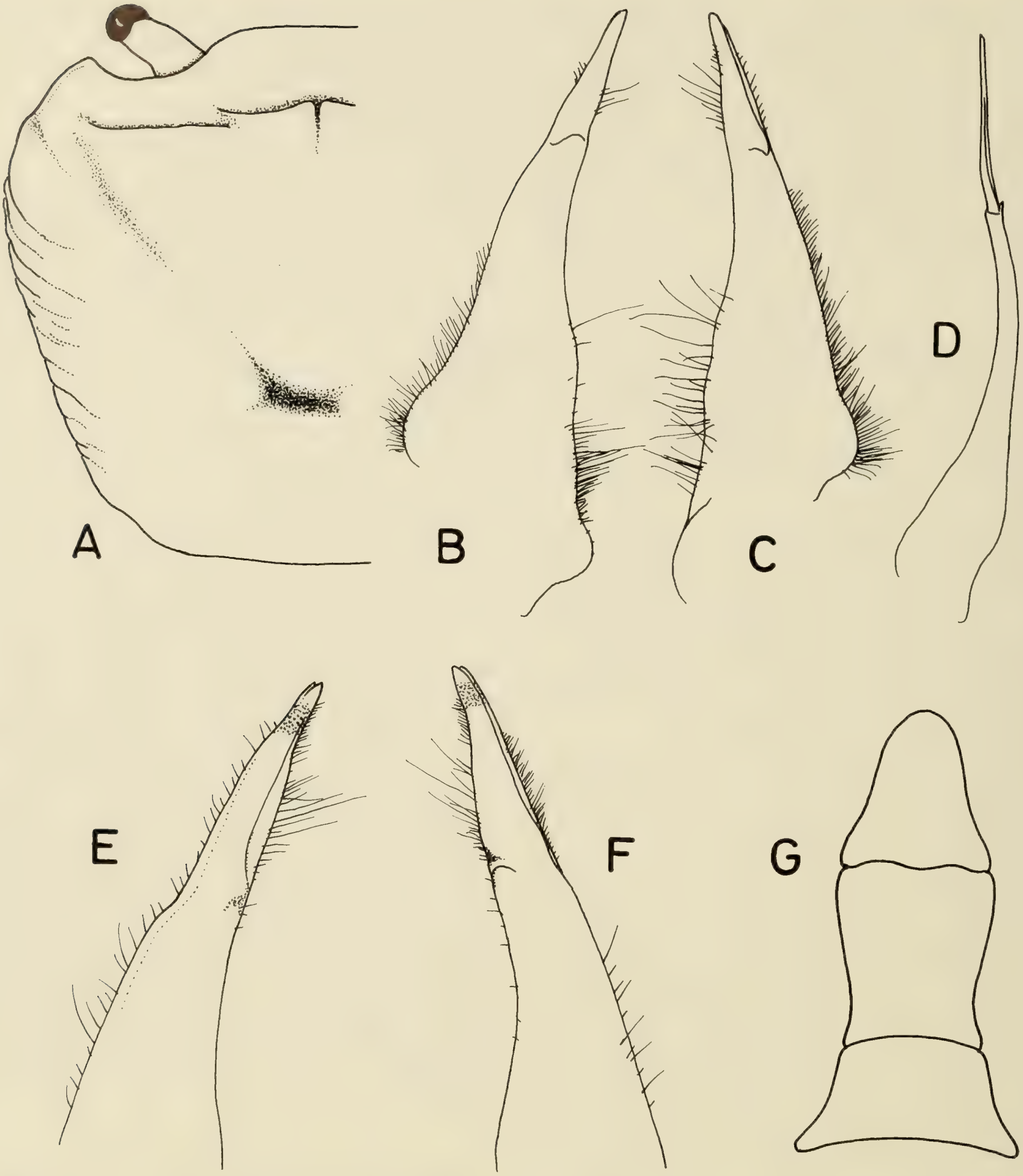

Fig. 3. *Irmengardia nemestrinus,* new species. Holotype, 16.9 by 14.5 mm, ZRC, Batam. A, left side of carapace; B, C, E, F, left G1s; D, left G2; G, last three abdominal segments. (B, E, ventral views; C, F, dorsal views; E, F, distal part of G1)

gle broad, truncate, outer margin convex to gently sinuous, about 3 times length of inner margin, not clearly separated from anterolateral margin; epibranchial tooth very low, indistinct; antero- and posterolateral margins not clearly demarcated, posterolateral margins with distinct oblique striae. Cervical groove shallow; H-shaped median depression deep. Epigastric cristae sharp, sinuous, slightly anterior to postorbital cristae, separated by deep cleft; postorbital cristae not very sharp, distinct, subparallel to frontal margin, separated from epigastric cristae by distinct oblique groove.

Chelipeds distinctly unequal in large males; larger male chela very high, appears laterally flattened, outer surfaces finely granulose; fingers shorter than palm, broad, blade-like, especially pollex; fingers of smaller chela longer than palm, not flattened or blade-like. Carpus with sharp spine on inner distal angle; merus with short sharp subdistal spine on upper margin.

Second ambulatory leg longest, with distinct acute subterminal spine on each dorsal meral margin.

Suture between sternal segments 2 and 3 very faint. Male abdomen distinctly T-shaped, segment 7 longer than segment 6, lateral margins of both segments distinctly concave.

G1 slender, directed outwards, terminal and subterminal segments clearly separated, outer margin of subterminal segment concave, terminal segment sharply tapering, about 0.32 times length of subterminal segment. G2 with distinct distal segment, 0.46 times length of basal segment.

Etymology.—The species is named after "Nemestrinus," the god of groves, alluding to the habitat of the species. The name is to be used as a noun in apposition.

Remarks.—The present new species is closely allied to *I. johnsoni* Ng & Yang, 1985, from Singapore, and the two species cannot be separated on external characters easily (cf. Ng 1988). The main external character is the width of the ambulatory dactylus, which in *I. johnsoni* is proportionately slightly wider. The G1s of the two species are quite different. The terminal and subterminal segments are more slender in *I. nemestrinus* (terminal segment 0.32 times length of subterminal segment; it is 0.45 for *I. johnsoni*), the terminal segment is straighter, and the outer margin of the subterminal segment is less concave (see Fig. 3E, F).

Ecology.—The specimens were all collected from a fast flowing stream with slightly tea-colored waters draining from a freshwater swamp forest. The substrate was mud and sand, and overgrown with the sedge *Eleocharis* sp. The edge of the stream was lined with dead ferns and leaves, and most of the specimens were collected from under this detritus.

Family Palaemonidae

Macrobrachium malayanum (Roux, 1936)

Material examined.—75 males, 16 females, ZRC, sites 2, 3, 4, Batam island, Riau Archipelago, Indonesia, leg. P. K. L. Ng, 29 Jan 1992.

Remarks.—This is the most common palaemonid freshwater prawn on Batam, and is present in every unpolluted freshwater stream which was sampled. The largest male (bl 64.3 mm, cl 18.6 mm, rl 10.4 mm) collected is the largest specimen of this species known thus far. The largest specimen known hitherto is the holotype of *M. geron* Holthuis, 1950 (bl 61 mm), which was synonymized with *M. malayanum* by Chong & Khoo (1987). The specimens of this species at Batam tend to have consistently shorter and more cup-like carpi, and in this respect, resemble *M. pilimanus* (De Man, 1879) and its allies. However, the pubescence on the larger male chela, form of the uropod, and rostrum, correspond best with *M. malayanum.*

Macrobrachium trompii (De Man, 1898)

Material examined.—2 males, ZRC, site 2, southwestern Batam island, Riau Archipelago, Indonesia, leg. P. K. L. Ng, 29 Jan 1992.

Remarks.—Only two specimens of this species were obtained from one area in Batam. This species is normally associated with forest streams and more acid waters (see Johnson 1966, 1968). One of the specimens (bl 76.7 mm, cl 22.5 mm, rl 12.8 mm) is the largest of this species known thus far (see Ng & Chong 1992).

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A REASSESSMENT OF *PAGURUS TRICARINATUS* (STIMPSON, 1858) (CRUSTACEA: DECAPODA: ANOMURA: PAGURIDAE)

Patsy A. McLaughlin

Abstract.—*Pagurus tricarinatus* (Stimpson) is redescribed and is illustrated for the first time. The presence, in females, of paired first pleopods modified as gonopods requires that this taxon be removed from *Pagurus.* In female morphology this species agrees well with *Ceratopagurus*; however, as males have not been described, it can only be transferred provisionally to this genus.

Stimpson (1858) described a new taxon, *Eupagurus tricarinatus* based on a single specimen of unspecified sex from Kagosima Bay, Japan. That specimen was presumably lost, with much of Stimpson's other materials, in the Chicago fire of 1871 (cf. Rathbun 1883). Although Stimpson's (1858) description (repeated in a posthumous publication in 1907) was brief and not accompanied by an illustration, the taxon was clearly defined by three crenulated keels on the dorsal surface of each chela. However, a superficially similar species, *Eupagurus triserratus,* having three spinose ridges on the right chela was subsequently described by Ortmann (1892) from Sagami Bay, Japan. Ortmann distinguished his species from Stimpson's (1858) by the absence of a rostrum in this latter species.

In their redescription and assignment of Ortmann's (1892) taxon to *Australeremus,* McLaughlin & Gunn (1992) noted that these two seemingly similar Japanese species had been reported and probably confounded by several authors. McLaughlin & Gunn reviewed the published records of each species and concluded that most, if not all of those records actually pertained to *A. triserratus.*

Supplemental to Ortmann's (1892) type material and the specimens from the Bonin Islands that Melin (1939) subsequently used to redescribe *A. triserratus,* McLaughlin & Gunn (1992) examined a specimen from the South China Sea from the Franz B. Steiner collection belonging to the California Academy of Science (CAS). A continuing study of that collection has now provided two specimens, both females, of Stimpson's *P. tricarinatus.* As was the case in Ortmann's (1892) taxon, females of Stimpson's (1858) species have paired first pleopods, modified as gonopods. Consequently *P. tricarinatus* too must be removed from the genus *Pagurus.* In the conformation of the cephalic shield and appendages, the unarmed sternite of the third maxillipeds, the shapes of the sternites of the third and fifth pereopods, the subequal chelipeds, the elongate and slightly twisted dactyls of the ambulatory legs, the single row of scales on the propodal rasps of the fourth pereopods, and general configuration of the telson, this species agrees with *Ceratopagurus* as redefined by McLaughlin (1988). However, until males are known, Stimpson's (1858) taxon can only be provisionally assigned to this genus.

Ceratopagurus tricarinatus (Stimpson, 1858)
Figs. 1, 2

Eupagurus tricarinatus Stimpson, 1858:251 [89]; 1907:228.—Ortmann, 1892:309.—Alcock, 1905:177.—Balss, 1913 (? in part):52, ? not 58 (see remarks).—Terao, 1913:372.

Pagurus tricarinatus: Gordon, 1956:336 (in part); see remarks.—McLaughlin & Gunn, 1992:90.

Not *Pagurus tricarinatus* Norman, 1869:264 [=*Pagurus alatus* Fabricius (cf. Ingle, 1985)].

Not *Eupagurus tricarinatus*: Sars, 1885:11, pl. 2, figs. 8–10.—Hansen, 1908:28 [=*Pagurus alatus* Fabricius (cf. Ingle, 1985)].

?Not *Pagurus tricarinatus*: Miyake, 1982: 197 [?=*Australeremus triserratus* (Ortmann, 1892)].

Material.—Taiwan Strait, South China Sea: 1 ♀ (shield length 2.4 mm), off Penghu Islands (Peng-hu Tao), 30–40 m, Apr 1971, coll. F. B. Steiner, CAS 046655; 1 ovigerous ♀ (shield length 4.2 mm), Formosa Bank, 50 m, Jul, 1973, coll. F. B. Steiner, CAS 046661.

Redescription.—Shield broader than long; anterior margin between rostrum and lateral projections concave; posterior margin truncate. Rostrum obsolete. Lateral projections produced, obtusely rounded and with terminal spinule. Interocular lobes ("bracteole" of Stimpson 1858) well developed. Ocular peduncles moderately short, equaling or slightly longer than shield but overreached by antennular peduncles; corneae strongly dilated. Ocular acicles developed into deeply grooved rectangular process armed with strong submarginal spine; separated basally by approximately entire width of 1 acicle.

Antennular peduncles with scattered setae on all 3 segments.

Antennal peduncles with scattered setae on fifth and fourth segments; third segment with small spine at ventrodistal angle; second segment with dorsolateral distal angle produced, terminating in small spine and with numerous long, stiff setae, dorsomesial distal angle with small spine; first segment produced ventrally and with 3 or 4 small spines laterally. Antennal acicle long, arcuate, terminating in small spine, mesial margin with long stiff setae.

Right and left chelipeds subequal, shorter than ambulatory legs. Dactyl of right cheliped ⅘ to approximately as long as palm; cutting edge with 3 or 4 large calcareous teeth in proximal half, row of small corneous teeth in distal half; terminating in small corneous claw; dorsomesial margin with row of very blunt spiniform processes, dorsal surface unarmed but with few scattered setae, mesial and ventral surfaces with scattered tufts of setae. Palm ⅔–¾ length of carpus; dorsomesial margin elevated into prominent crenulated keel, dorsal midline and dorsolateral margins each also with prominently elevated, crenulated keel extending almost entire length of fixed finger, crenulations becoming more tuberculate or spiniform on fixed finger; dorsal surface between keels unarmed; cutting edge of fixed finger with strong calcareous teeth in proximal ⅔, small calcareous teeth interspersed with minute corneous teeth in distal third, terminating in small corneous claw; mesial, lateral and ventral surfaces all with short, transverse rows of long, stiff setae. Carpus with somewhat trapezoidal dorsal surface, dorsomesial margin with row of moderately small acute spines, second irregular row of somewhat smaller spines traversing dorsal surface from midline distally to dorsolateral margin proximally; all surfaces with short, transverse rows of long stiff setae. Merus subtriangular; approximately ⅔ length of carpus; dorsal margin with few tufts of long setae in transverse rows; mesial and lateral faces with short, transverse rows of long stiff setae in ventral halves, ventromesial and ventrolateral margins each 1 or 2 spines and tufts of long stiff setae. Ischium with 2 small tubercles on ventral margin proximally.

Left cheliped with dactyl slightly longer than palm; cutting edge with row of very closely spaced corneous teeth; terminating in corneous claw; dorsomesial margin with row of blunt spines or tubercles, decreasing in size distally; mesial and ventral surfaces with scattered tufts of long stiff setae. Palm with dorsomesial margin elevated into prominent crenulated keel, dorsal midline

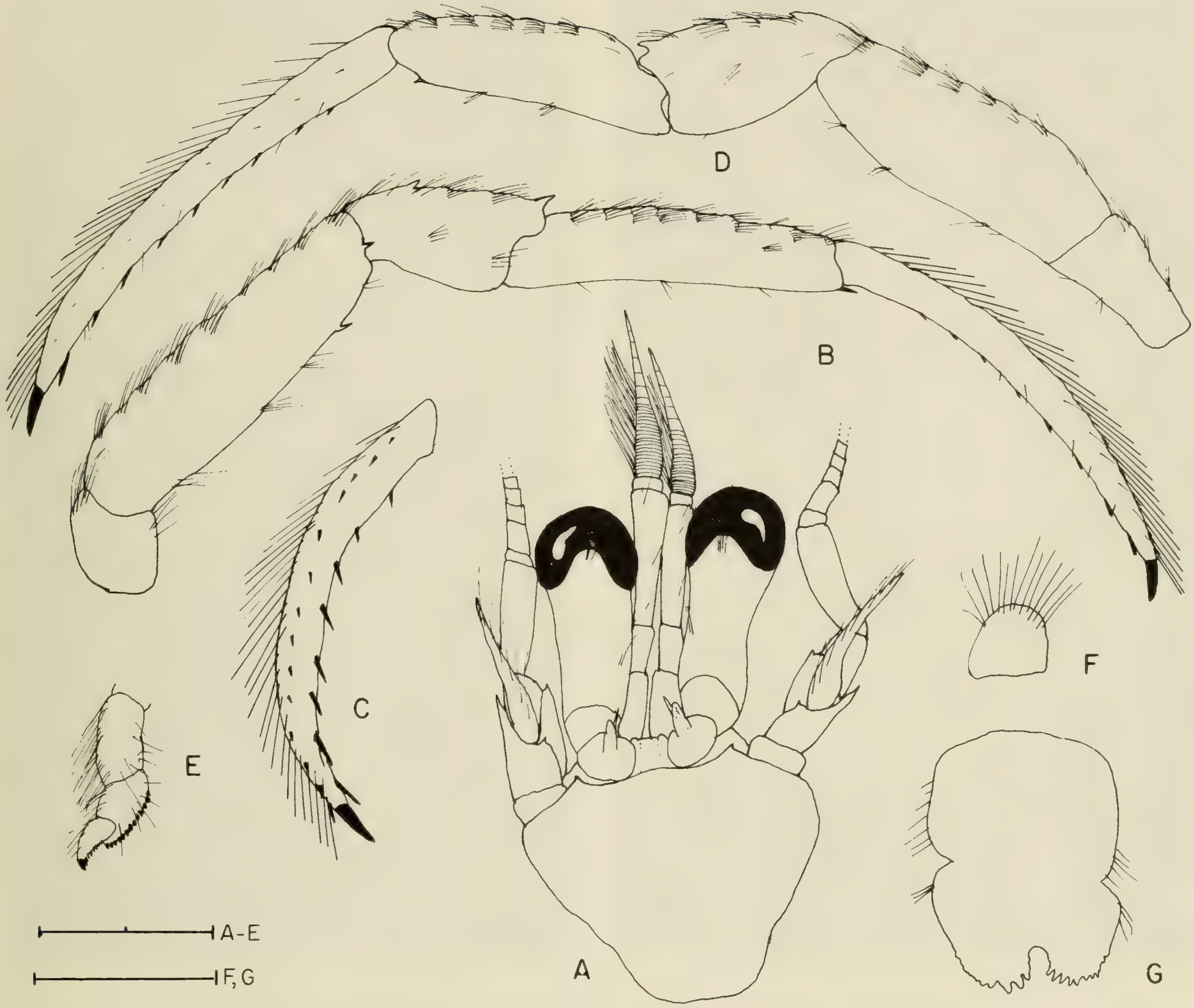

Fig. 1. *Ceratopagurus tricarinatus* (Stimpson, 1858), female, CAS 046661. A, Shield and cephalic appendages. B, Right second pereopod, lateral view. C, Dactyl of right second pereopod, mesial view. D, Left third pereopod, lateral view. E, Left fourth pereopod, lateral view. F, Anterior lobe of sternite of third pereopods. G, Telson. Scales equal 2.0 mm, A–E and 1.0 mm, F, G.

and dorsolateral margins each with prominent, elevated and crenulated keel extending onto fixed finger and becoming more spiniform, dorsal surface unarmed except for 1 or 2 small spines at articulation of dactyl and fixed finger; mesial, lateral and ventral surfaces all with short, transverse rows of long stiff setae; cutting edge of fixed finger with row of evenly-spaced small calcareous teeth. Carpus slightly longer than merus; dorsomesial margin with row of moderately small spines, dorsolateral margin with shorter row of somewhat smaller spines practically obscured by tufts of long setae; lateral and mesial faces each with short transverse rows of long stiff setae, ventrolateral margin with 1 or 2 spines or tubercles distally, ventral margin with transverse, sometimes spinulose ridges and long stiff setae. Merus subtriangular; dorsal margin with few transverse rows of setae; ventrolateral margin with 2 or 3 acute spines, ventrodistal margin with 1 to several small spinules or tubercles, ventromesial margin with 2 or 3 acute spines; lateral and mesial faces with short transverse rows of long stiff setae. Ischium with row of minute spinules on ventral margin and 2 slightly larger tubercles proximally.

Second and third pereopods elongate,

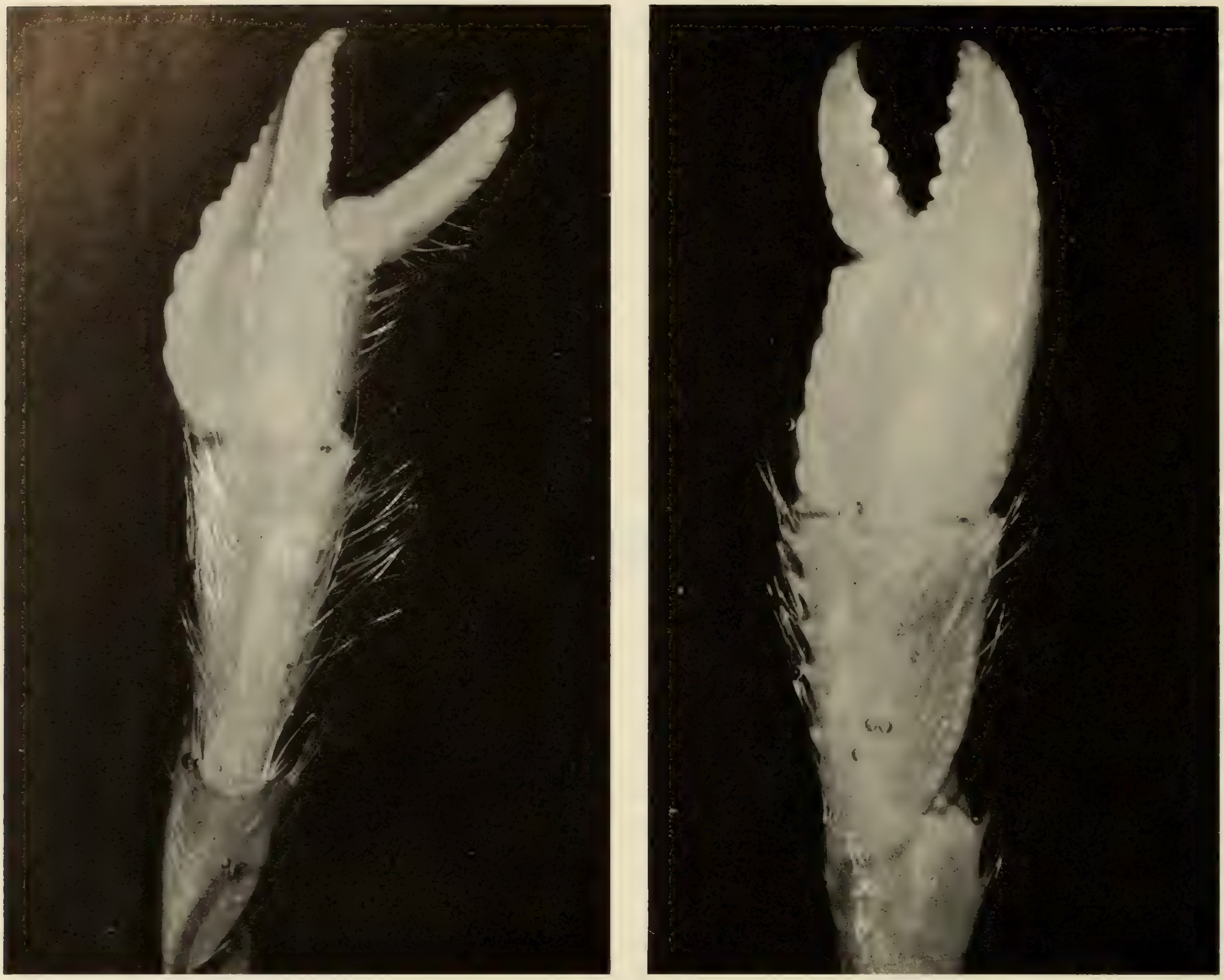

Fig. 2. *Ceratopagurus tricarinatus* (Stimpson, 1858), female, CAS 046661. Left, Left cheliped. Right, Right cheliped. 11× Magnification.

generally similar from left to right. Dactyls at least half again length of propodi; in dorsal view, slightly twisted; in lateral view, slightly curved ventrally; dorsal surfaces each with row of long stiff bristles becoming spiniform in distal half and accompanied by short corneous spines, increasing in size distally, lateral faces with row of very short setae, mesial faces each with row of corneous spinules dorsally, ventral margin proximally and ventromesial margin distally with row of corneous spines, increasing in size distally. Propodi 1¼ to twice length of carpi, dorsal margins each with short transverse rows of long setae, ventral margins tufts of setae and corneous spine at distal margin. Carpi ½ to ⅔ length of meri; dorsal surfaces each with spine at distal margin and 1 smaller spine in proximal third. Meri with tufts of setae on dorsal and ventral margins, second pereopods also with 1 acute spine on distolateral margin and 1 spine on ventral margin distally. Ischia with few tufts of setae dorsally and ventrally.

Sternite of third pereopods with row of long setae on subquadrate anterior lobe.

Uropods markedly asymmetrical. Telson with transverse suture; posterior lobes with prominent median cleft; terminal margins each with row of small spines extending onto lateral margins.

Distribution.—Japan and Taiwan, to 50 m.

Remarks.—In a report on East Asian decapods, Balss (1913) provided a key to the Japanese species of *Pagurus* (as *Eupagurus*) which accurately distinguished both *Ceratopagurus tricarinatus* and *Australeremus triserratus,* although the latter species was not mentioned in his species account. Balss did identify a single female from Sagami Bay as *E. tricarinatus,* remarking that Stimpson's (1858) taxon was only a variety of the European species *Eupagurus excavatus* (Herbst). However, his comment that his specimen differed from Stimpson's (1858) description by the presence of a distinct rostral spine led McLaughlin & Gunn (1992) to suspect that Balss's (1913) specimen was actually *A. triserratus.*

Norman (1869) described a new species of hermit crab from the Atlantic Shetland Islands as *Pagurus tricarinatus,* not realizing that the name was preoccupied by Stimpson's Pacific taxon. *Pagurus tricarinatus* sensu Norman was also used by Sars (1885) for a species collected off Norway, and by Hansen (1908) for specimens collected in the North Atlantic. However, A. Milne Edwards & Bouvier (1892) placed Norman's (1869) *P. tricarinatus* in synonymy with *P. excavatus* (Herbst). In contrast, Hansen (1908) thought it might be the senior synonym of *P. variabilis* (A. Milne Edwards & Bouvier). Forest (1955) considered *P. excavatus,* Norman's *P. tricarinatus, P. meticulosus* Roux, and *P. angulatus* Risso all synonyms of *P. alatus* Fabricius. Gordan's (1956) bibliographic citation of *P. tricarinatus* included authors that were referring to both the Atlantic and Pacific taxa. The confusion over the identities of the Atlantic species was finally resolved by Ingle (1985).

As pointed out by McLaughlin & Gunn (1992), Miyake (1978, 1982) was uncertain about the distinctiveness of *A. triserratus* and *C. tricarinatus.* In his "Anomura of Sagami Bay," Miyake (1978) accurately figured and briefly described *A. triserratus* (as *Pagurus*); however, in his index to the species, he questionably equated it to *C. tricarinatus* (as *Pagurus*). In his subsequent publication on Japanese crustaceans, Miyake (1982) listed the taxon as *P. tricarinatus* [?=*P. triserratus*]. Based upon his 1978 description and figure, it appears that Miyake's references to *P. tricarinatus* pertain to *A. triserratus.*

Among Pacific pagurids, *C. tricarinatus* is singularly distinctive. The dorsal crenulated keels of both chelae set it apart from all other described species, although a superficial similarity does exist with the Atlantic species *P. alatus* and *P. excavatus.* All three taxa lack rostrums, have relatively short, stout ocular peduncles, spinose posterior telsonal lobes, and keeled right chelae. However, both Atlantic species have triangular, spinose anterior lobes of the sternite of the third pereopods, grossly unequal chelipeds and lack female paired first pleopods modified as gonopods. There is also a distinct difference in the morphology of the keels between the Atlantic species and *C. tricarinatus.*

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A REVIEW OF THE GENUS *CHLORONIA* IN COSTA RICA, WITH THE DESCRIPTION OF TWO NEW SPECIES (NEUROPTERIDA: MEGALOPTERA: CORYDALIDAE)

Oliver S. Flint, Jr.

Abstract.—The genus *Chloronia,* containing 10 previously described species, is limited to the Neotropical Region. Recent large collections from Costa Rica reveal the presence of 5 species in the country. *Chloronia mexicana* and *C. gloriosoi* are recorded for the first time from Costa Rica, and *C. absona* and *C. osae* are herein described. *Chloronia mirifica* is the most frequently encountered species and the only one previously recorded from Costa Rica.

The genus *Chloronia* is found only in the Neotropical Region, where, because of its color (yellow marked with black spots), it is one of the most easily recognized genera of the family. Penny & Flint (1982) revised the genus, recognizing ten species and providing a superficial description of the larva for the first time. At that time only one species, *C. mirifica* Navás, 1925, was known from Costa Rica. During the eighties, with extensive collecting in Costa Rica as part of numerous biosystyematic surveys initiated by Drs. Janzen and Holzenthal, more material of this genus was obtained. This has recently been forwarded to me for study, with rather surprising results: the number of species known from Costa Rica has increased to five of which two are new to science.

Chloronia mexicana Stitz, 1914, known previously from eastern Mexico south into central Guatemala, is recorded for the first time from Costa Rica, where it is quite common in the drier northwestern corner. *Chloronia gloriosoi* Penny & Flint, 1982, otherwise known only from the type series taken in the mountains of northern Panama, was found in the wet mountains of central Costa Rica. The new species, *C. absona,* is known from several pluvial, forest sites in the mountains of northern and central Costa Rica. The second new species, *C. osae,* is recorded from two wet forests sites, one in the lowlands of the Osa Peninsula, the other much higher in the mountains, both localities near the southern border of the country. *Chloronia mirifica* has the greatest known distribution of any of the Costa Rican species, being known from Mexico south into Ecuador, at least, and is the most frequently encountered species in wet, forest sites in mountainous and hilly country.

The following key to the Costa Rican species primarily utilizes characters of the male genitalia because coloration will only reliably separate *C. mexicana.*

Key to Costa Rican Species

1 Apical two-thirds of antenna infuscate, forewings with conspicuously darkened cross-veins, but with virtually no other dark marks apicad of the basal spots .... *C. mexicana*
– Only apical third or less of antenna infuscate, forewings with both cross-veins blackened and with conspicuous dark marks in membrane 2
2 Male genitalia with ninth gonostyli divided into a distinct basolateral, thumb-like lobe and a large mesal lobe .... *C. absona*

– Ninth gonostyli entire, a simple clavate lobe 3

3 Male genialia with ninth tergum lacking small rows of short, dark setae, tenth gonostyli broadly trianguloid ending in a sharp apicomesal point .... *C. mirifica*

– Ninth tergum with two pairs of rows of short, dark setae; tenth gonostyli rounded, lobes about as long as broad 4

4 Male genitalia with ninth sternites roughly quadrate, posterior margin with an obtuse angle laterad ... *C. osae*

– Ninth sternites produced both basolaterally and posteromesally..... .... *C. gloriosoi*

Chloronia gloriosoi Penny & Flint
Fig. 1

Chloronia gloriosoi Penny & Flint, 1982:11.

This species had been known previously only from Fortuna in northern Panama, a wet forested site at 1050 m elevation on the western slope of the Cordillera Central. A single male has been taken in the Cordillera Central in Costa Rica.

Material.—Costa Rica [San José Province], Fila Carrillo, Parque Nacional Braulio Carrillo, 18 May 1984, A. Chacón, 1 ♂ (INBIO).

Chloronia mexicana Stitz
Fig. 1

Chloronia mexicana Stitz, 1914:199.—Penny & Flint, 1982:13.

This is an easily distinguished species; the color of the antennae and the wings (see key) permit recognition of examples of both sexes. The male genitalia (Penny & Flint 1982, figs. 34–36) are very distinctive, albeit very close to those of *C. pallida* (Davis), which may be no more than a color variant. In 1982 we had examples from no further south than northwestern Guatemala; the discovery of the species in northern Costa Rica is thus a major range extension.

Material.—Costa Rica, Guanacaste Province, Hacienda Tempisquito (Pelón de la Altura), 1 km NE km 254, Rt. 1, 10.84°N, 85.56°W, 100 m, 18 Jul 1987, Holzenthal, Morse & Clausen, 2 ♂, 6 ♀ (NMNH & UMSP); same data, except, Jun 1989, C. de la Rosa, 2 ♂, 1 ♀ (EBM). Río Tempisquito, Estación Maritiza, W side Volcán Orosí, 18 km E Rt. 1, 10.958°N, 85.497°W, 550 m, 2 Jun 1989, C. de la Rosa, 1 ♀; same data, except, 9 Jun 1989, 1 ♀; same data, except 5 Jul 1989, 1 ♀; same data, except 6 Jul 1989, 1 ♀ (EBM); same data, except Jul 1989, GNP Biodiversity Survey, 2 ♀ (INBIO). Finca Jenny, 31 km N Liberia, 10°51′55″N, 85°34′27″W, 300 m, Sep 1988, GNP Biodiversity Survey, 3 ♀ (NMNH & INBIO). Santa Rosa National Park, 5–7 Jun 1980, Janzen & Hallwachs, 1 ♀ (INBIO); same data, except 14–16 Jun 1980, 1 ♂ (INBIO).

Alajuela Province, Río Pizote, ca. 5 km (air) S Brasilia, 10.972°N, 85.345°W, 390 m, 12 Mar 1986, Holzenthal & Fasth, 2 ♀ (UMSP). Río Pizote, ca. 5 km N Dos Ríos, 10.948°N, 85.291°W, 470 m, 9 Mar 1986, Holzenthal & Fasth, 1 ♀ (NMNH). Finca San Gabriel, 2 km SW Dos Ríos, 600 m, Jun 1989, GNP Biodiversity Survey, 1 ♀ (INBIO).

Heredia Province, Río Peje, Estación El Ceibo, Parque Nacional Braulio Carrillo, 10.327°N, 84.078°W, 480 m, 29–31 May 1990, Holzenthal, Blahnik & Muñoz, 1 ♀ (NMNH).

Chloronia mirifica Navás
Fig. 2

Chloronia mirifica Navás, 1925:195.—Penny & Flint, 1982:10.

The neotype of this species is from Costa Rica where it appears to be the most commonly encountered species. It is also known from Mexico, Guatemala, Colombia, Ecuador, and Peru (a record based on a female

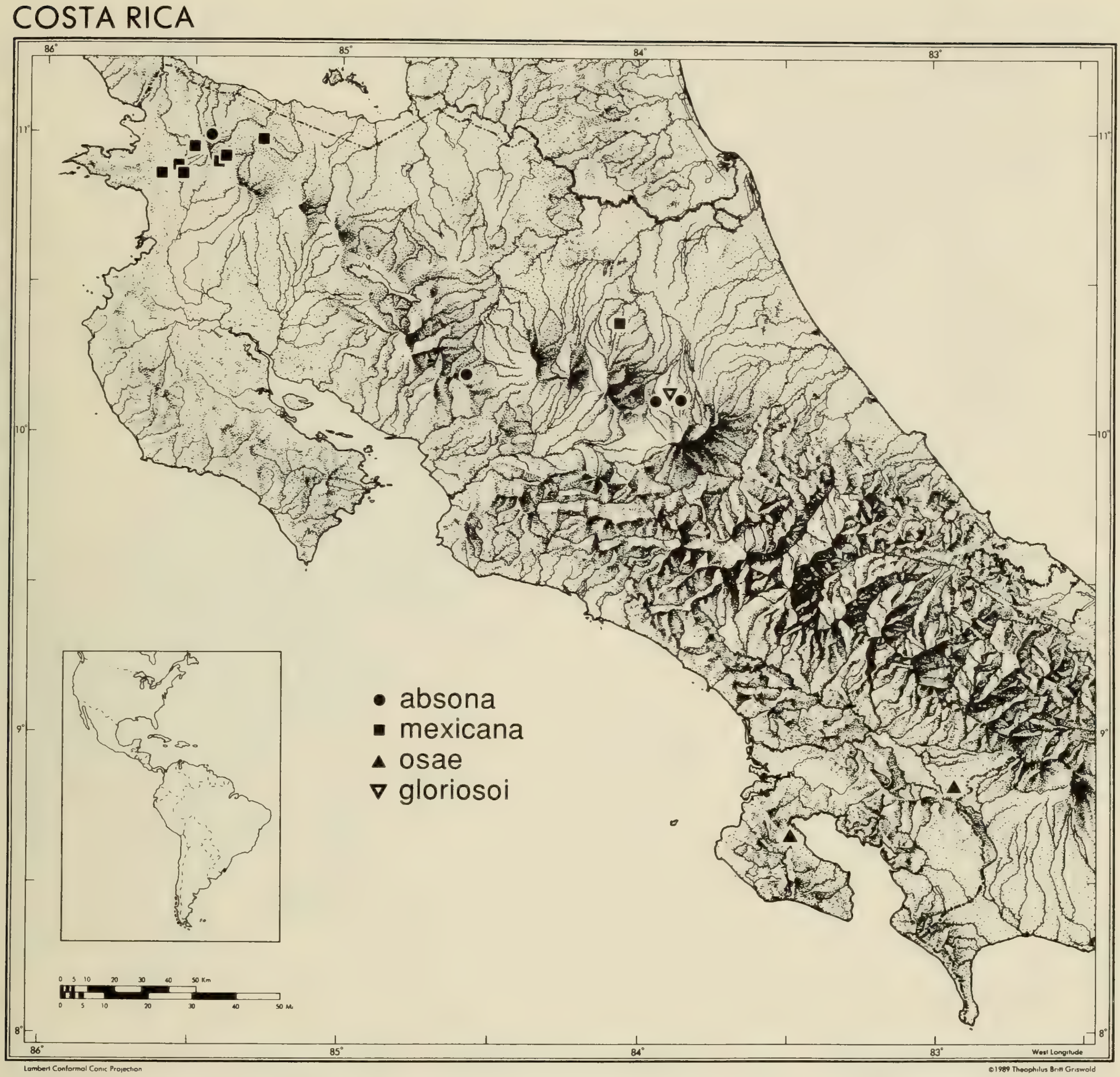


Fig. 1. Distributions of *Chloronia absona, C. mexicana, C. osae* and *C. gloriosoi* in Costa Rica.

that needs a male for verification). The earlier Costa Rican records are from the provinces of Alajuela (Aguas Zarcas) and Cartago (Tuís, Peralta and Juan Viñas).

Material.—Costa Rica, Alajuela Province, tributary Río Bochinche, Cerro Campana, ca. 6 km (air) NW Dos Ríos, 10.945°N, 85.413°W, 640 m, 15–16 Mar 1986, Holzenthal & Fasth, 2 ♂, 1 ♀ (UMSP); same data, except 22–23 Jul 1987, Holzenthal, Morse & Clausen, 2 ♀ (UMSP). Río San Lorencito and tributaries, Reserva Forestal San Ramón, 10.216°N, 84.607°W, 980 m, 1–4 May 1990, Holzenthal & Blahnik, 1 ♂ (UMSP); same data, except 13–16 Jun 1988, C. M & O. S. Flint, Jr. & Holzenthal, 1 ♂, 2 ♀ (NMNH); same data, except 4 May 1984, A. Solis Blanco, 2 ♂ (INBIO); same, data except 24 May 1986, 1 ♀ (INBIO).

Guanacaste Province, Río Tempisquito, Estación Maritiza, W side Volcán Orosí, 18 km E Rt. 1, 10.958°N, 85.497°W, 550 m, 19–20 Jul 1987, Holzenthal, Morse & Clausen, 2 ♀ (UMSP); same data, except 17–18

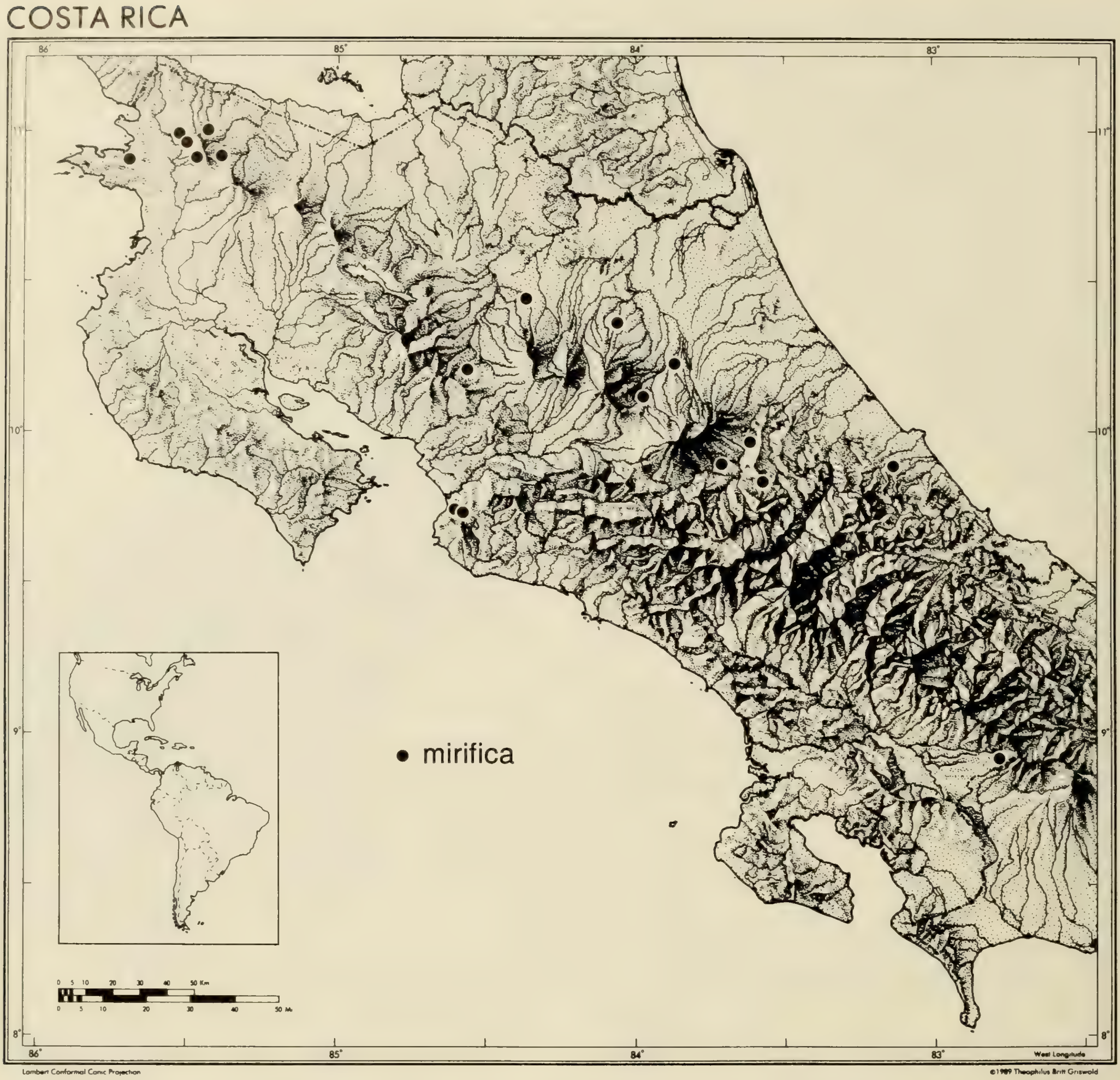


Fig. 2. Distribution of *Chloronia mirifica* in Costa Rica.

Jun 1988, C. M & O. S. Flint, Jr. & Holzenthal, 1 ♂, 8 ♀ (NMNH); same data, except 30 May 1989, C. de la Rosa, 1 ♂; same data, except 2 Jun 1989, 2 ♂, 1 ♀; same data, except 6 Jun 1989, 2 ♂, 4 ♀; same data, except 10 Jun 1989, 1 ♀; same data, except 23 Jun 1989, 1 ♀; same data, except 25 Jun 1989, 1 ♂, 1 ♀; same data, except 26 Jun 1989, 1 ♂, 1 ♀; same data, except 4 Jul 1989, 4 ♂, 6 ♀; same data, except 5 Jul 1989, 4 ♂, 9 ♀; same data, except 6 Jul 1989, 7 ♂, 10 ♀; same data, except 11 Sep 1989, 2 ♀ (EBM); same data, except Jun 1988, Janzen & Hallwachs, 1 ♂, 8 ♀ (INBIO); same data, except GNP Biodiversity Survey, 3 ♂, 5 ♀ (INBIO); same data, except Jul 1989, 3 ♂, 15 ♀ (INBIO). Río Sapoá, water dam near Estación Cerro El Hacha, 14 Jul 1989, C. de la Rosa, 1 ♀ (EBM). Río Orosí, Estación Pitilla, 10.991°N, 85.428°W, 700 m, 19–20 Jun 1988, C. M & O. S. Flint, Jr. & Holzenthal, 1 ♀ (NMNH); same data, except 11 Mar [no year or collector], 1 ♂; same data, except May 1988, GNP Biodiversity Survey, 1 ♂, (INBIO); same data, except Jul 1988, 2 ♂, 2 ♀ (INBIO); same data, except Sep 1988, 1 ♀ (INBIO); same data, except Oct 1988, 2 ♀ (INBIO); same data, except Nov 1988, 1 ♀ (INBIO); same data, except Mar 1989, 1 ♂ (INBIO); same data, except 21 Mar–21 Apr 1989, 1 ♂ (INBIO); same data, except May 1989, 3 ♂ (INBIO). Vicinity Estación Murcielago, 8 km SW Cuajiniquil, 100 m, Jun 1989, GNP Biodiversity Survey, 1 ♂, 1 ♀ (INBIO). Estación Cacao, SW side Volcán Cacao, 1000–1400 m, Sep 1989, R. Blanco & C. Chavez, 2 ♀ (INBIO).

Heredia Province, Estación El Ceibo, Parque Nacional Braulio Carrillo, 400–600 m, Sep 1989, R. Aguilar & M. Zumbado, 1 ♂, 2 ♀ (INBIO); same data, except Oct 1989, 2 ♀ (INBIO); same data, except Nov 1989, 1 ♀ (INBIO).

Limón Province, Quebrada Gonzalez, Parque Nacional Braulio Carrillo, 10.160°N, 83.939°W, 480 m, 12–14 May 1990, Holzenthal & Blahnik, 5 ♂, 5 ♀ (UMSP). Río Segundo [9°53′00″N, 83°13′20″W], afluente Río Banano, 500 m, 28 Apr 1985, A. Solis, 1 ♀ (INBIO).

Puntarenas Province, Estación Quebrada Bonita, Reserva Biológica Carara, 50 m, Nov 1989, R. Zuniga, 1 ♀ (INBIO); same, except Estación Bijagual, 500 m, 1 ♀ (INBIO); same, except Jan 1990, 1 ♀ (INBIO). Finca Cafrosa, Estación Las Mellizas, Parque Nacional La Amistad, 1300 m, 20 Aug–4 Sep 1989, M. Ramirez & G. Mora, 1 ♂, 1 ♀ (INBIO).

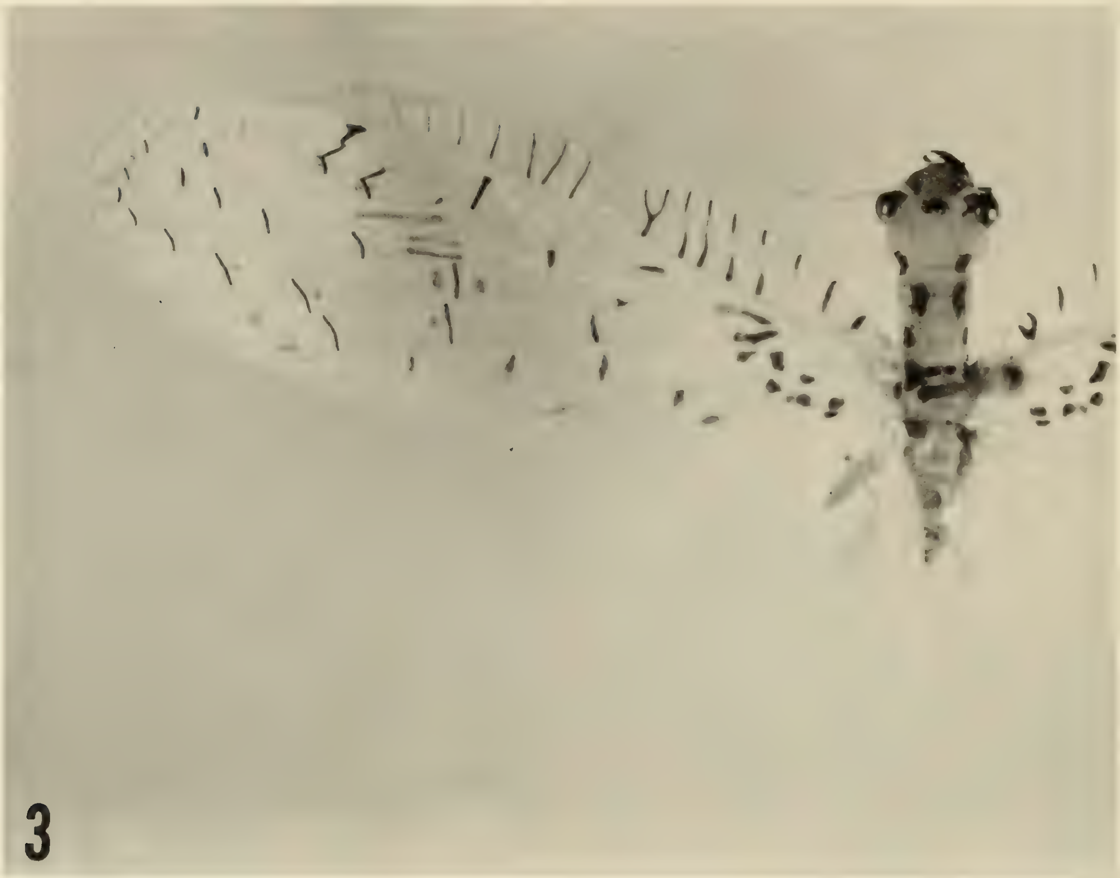
San José Province, La Montura, Parque Nacional Braulio Carrillo, 1100 m, 20 Mar 1983, R. L. Hestelberg, 1 ♂, 1 ♀ (INBIO).

Chloronia osae, new species
Figs. 1, 3, 5–7

This species appears to be quite closely related to *C. antilliensis* Flint, known for certainty only from the island of Dominica in the Lesser Antilles. It differs quite strongly from *C. antilliensis* by having more strongly spotted forewings, especially near their bases. The male genitalia of the two species are very similar. The most distinctive differences being in the possession of three pairs of tufts of spinous setae dorsally in *C. osae* (two pairs on the ninth tergites and one basally on the tenth tergite), but only one pair in *C. antilliensis* (on the ninth tergite). The tenth segment gonostyli are a bit longer and the gonocoxites are a bit broader in *C. osae* than in *C. antilliensis.* The ninth sternum in *C. osae* lacks any development of the lateral lobe, which is present, although rather small, in *C. antilliensis.*

Adult.—Length of forewing 31–32 mm. Color generally pale yellow with fuscous spots. Head pale yellow with fuscous ocellar triangle, compound eyes, distal half of mandibles, labial and maxillary palpi. Two fuscous spots at posterior margin of occiput. Antenna with basal 25 segments pale yellow; apical 8–10 segments fuscous. Pronotum pale yellow, the 2 anterior and 2 posterior spots fuscous; mesonotum with 2 anteromesal and 2 lateral fuscous spots. Forewing pale yellow with costal crossveins wholly or at ends and all crossveins fuscous, a band of conspicuous very dark spots basad, some marking in membrane in radial and medial cells, but marginal cells with dark spots much reduced. Hindwing wholly pale yellow except for 2nd *r* fuscous. Male genitalia: Ninth tergum with anterior margin with broad, U-shaped, excision mesally about third depth of tergum; each tergite with 2 patches of short, spinous setae. Ninth sternite quadrate, with small lobe on posterior margin. Tenth tergite long, parallel-sided, slightly curved, with small, basal patch of enlarged, spinous setae. Ninth gonostylus incurved, hardly inflated apicad, with sharp apical point. Tenth gonostylus rounded, about twice as long as broad, connected by bandlike gonocoxite.

Material.—Holotype, male: Costa Rica, Puntarenas Province, Osa Peninsula, 2.5 mi SW Rincón, 8°42′N, 83°29′W, 1–7 Mar 1967, OTS advanced zoology course. INBIO Type. Paratype: [Costa Rica, Puntare-



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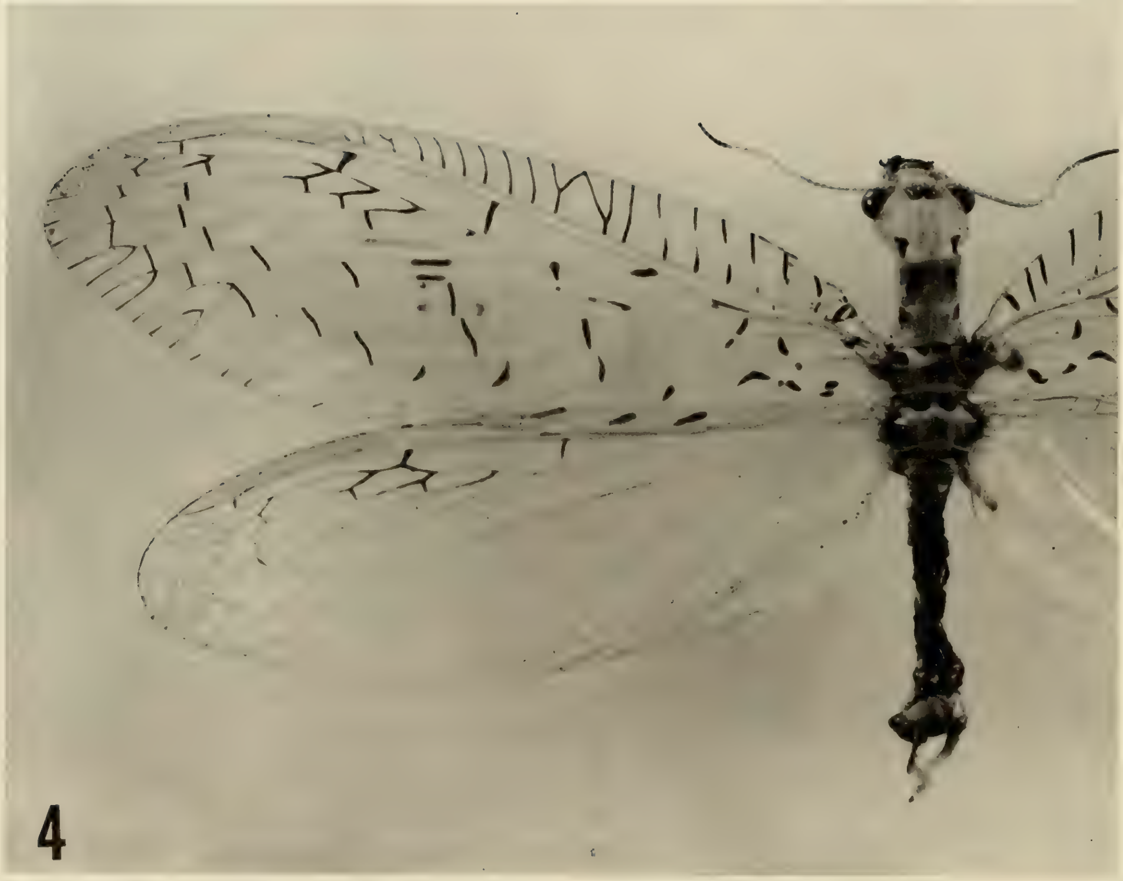

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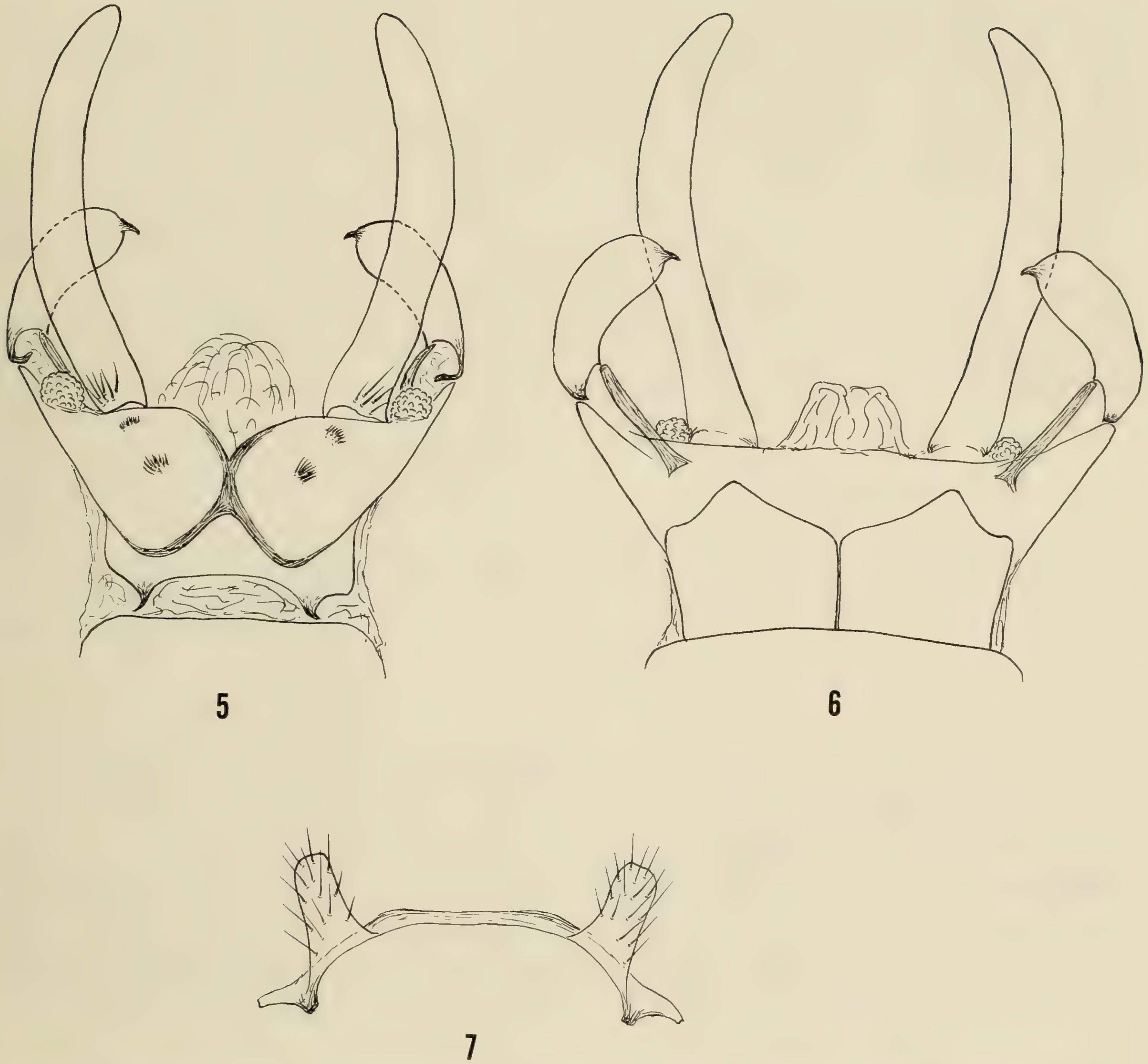
Figs. 3–4. Habitus: 3, *Chloronia osae*; 4, *C. absona*.



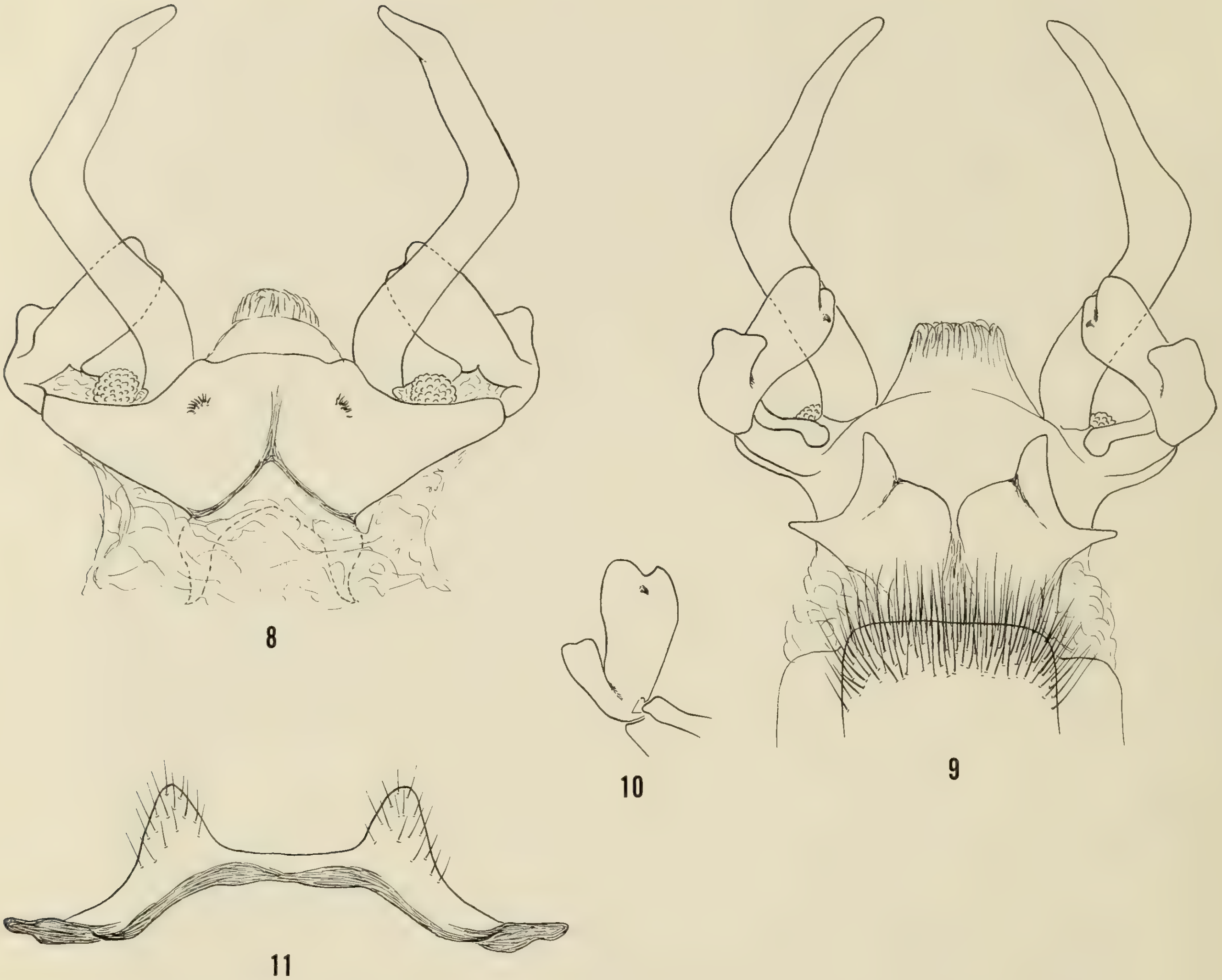
Figs. 5–7. Male genitalia of *Chloronia osae*: 5, dorsal; 6, ventral; 7, tenth gonocoxite and gonostyli.

nas Province], Las Cruces [Jardín Botánico Las Cruces, 6 km S San Vito on Rt. 16, ca. 1000 m], Sep 1986, L. D. Gómez, 1 ♂ (NMNH).

Chloronia absona, new species
Figs. 1, 4, 8–11

The male genitalia of this species are the most highly modified of any species yet known in the genus, making the relationships very difficult to determine. On the basis of the bilobate ninth sternites and rather broadly rounded tenth gonostyli it would seem to fit in with *C. mirifica* and *C. gloriosoi.* The long, angulate tenth tergites, produced, hairy eighth sternum, and above all the strange ninth gonostyli with their basolateral process and enlarged, shallowly bilobed apex displacing the small apical hook mesad are unique to this species.

Adult.—Length of forewing male 41–44 mm (ave. 42.75 mm, 4 examples), female 40–48 mm (ave. 43 mm, 6 examples). Color generally waxy yellow with fuscous spots. Head yellow with fuscous ocellar triangle, compound eyes, distal half of mandibles, labial and maxillary palpi. Two fuscous spots at posterior margin of occiput. Antenna with



Figs. 8–11. Male genitalia of *Chloronia absona*: 8, dorsal; 9, ventral; 10, ninth gonostylus, mesal view; 11, tenth gonocoxite and gonostyli.

35–40 segments; yellow basally, apical fourth infuscate. Pronotum yellow, the 2 anterior and 2 posterior spots fuscous; mesonotum with 2 anteromesal and 2 lateral fuscous spots. Forewing waxy yellow with costal crossveins wholly or at ends and all crossveins fuscous, basad with black spots reduced (limited to crossveins or vein junctions), some faint marking in membrane in radial and medial cells, marginal cells with dark spots elongate and very faint. Hindwing pale yellow except for 2nd *r* and veins and crossveins immediately posteriad fuscous. Male genitalia: Ninth tergum with anterior margin with V-shaped, excision mesally more than half depth of tergum; each tergite with single patch of short, spinous setae. Eight sternum with posteromesal margin slightly produced into quadrate lobe and bearing brush of long setae along posterior. Ninth sternite with distinct lateral and posterior projections. Tenth tergite very long, angulate at midlength and tapering slightly apicad. Ninth gonostylus incurved, inflated, produced and shallowly bilobed apicad, with large, almost rectangular, thumb-like lobe basolaterally, apical sclerotized point small and displaced mesad. Tenth gonostylus tapering but rounded apicad, slightly longer than broad, connected by bandlike gonocoxite which extends well laterad of gonostyli.

Material.—Holotype, male: Costa Rica, Alajuela Province, Río San Lorencito and tributaries, Reserva Forestal San Ramón, 10.216°N, 84.607°W, 980 m, 1–4 May 1990, Holzenthal & Blahnik. NMNH Type. Paratypes: Same data, 1 ♂ (INBIO), 1 ♀ (NMNH); same, but 4 May 1987, A. Solis Blanco, 1 ♀ (INBIO). San José Province, Quebrada Sanguihuela, Parque Nacional Braulio Carrillo, 10.160°N, 83.963°W, 800 m, 27 Mar 1987, Holzenthal, Hamilton & Heyn, 1 ♂ (UMSP). Limón Province, Quebrada Gonzalez, Parque Nacional Braulio Carrillo, 10.160°N, 83.939°W, 480 m, 12–14 May 1990, Holzenthal & Blahnik, 1 ♂ (UMSP). Guanacaste Province, Pitilla, 9 km S Santa Cecilia, 700 m, 21 Mar–12 Apr 1989, P. Rios & C. Chaves, 1 ♂, 2 ♀ (NMNH); same, but May 1988, GNP Biodiversity Survey, 1 ♀ (INBIO); same, but Mar 1989, 1 ♀ (INBIO).

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CAPROVESPOSUS FROM THE OLIGOCENE OF RUSSIA: THE PELAGIC ACRONURUS PRESETTLEMENT STAGE OF A SURGEONFISH (TELEOSTEI: ACANTHURIDAE)

Alexandre F. Bannikov and James C. Tyler

Abstract.—*Caprovesposus parvus* Danilchenko (1960) from the Lower Oligocene of Russia was originally described in the Caproidae, Zeiformes. Bannikov & Fedotov (1984) placed it in the Perciformes as the Caprovesposidae, and noted the similarity between *Caprovesposus* and the pelagic larvae of the Acanthuridae, while Bannikov (1991) assigned the family to the Acanthuroidei.

Caprovesposus is shown to be the acronurus presettlement stage of an acanthurid. It has such derived features of the acanthurids as highly lobate teeth and a complex locking mechanism of the first two dorsal and anal spines. It also has primitive perciform features of head spination not found in the acronurus stages of any extant species of Acanthuridae.

Among the extensive and mostly oceanic pelagic ichthyofauna of the Lower Oligocene Maikopian (Maikop) deposits of northwestern Caucasus, Russia, reviewed by Danilchenko (1960) were a few small acanthopterygians that he described as the new genus and species *Caprovesposus parvus.* He placed it in the zeiform family Caproidae because of similarities to *Capros* in the number of vertebrae and in the form and position of the median fins. Because *Caprovesposus* had vertically elongate scales, Danilchenko believed that it also had affinities with the zeiform grammicolepidid *Vesposus* (a synonym of *Grammicolepis*) and proposed that "*Caprovesposus* possibly occupies an intermediate position between Caproidae and Grammicolepididae" and "possibly should be promoted into a family of the Order Zeiformes" (Danilchenko 1967: 100). Danilchenko gave the size range of his specimens as 24 to 55 mm total length. However, the five specimens in the Paleontological Institute in Moscow on which the description was based are no larger than about 40 mm total length and 30 mm SL. In addition, the scale for the illustration of the holotype is incorrect in that it indicates a specimen of over 100 mm SL while it is actually 19.2 mm SL.

Based on their examination of 26 specimens of *Caprovesposus parvus* from Oligocene Maikopian deposits, Bannikov & Fedotov (1984) established the new perciform family Caprovesposidae, showing that it differs greatly from the Caproidae by: 1) single dorsal fin; 2) dorsal spines all approximately the same length (except the first in the specialized locking mechanism); 3) lower supraoccipital crest; and 4) vertically elongate scales. Bannikov and Fedotov were uncertain whether to attribute this new family to the Percoidei or Acanthuroidei, and placed it *incertae sedis* in the Perciformes. However, they noted similarities between *Caprovesposus* and the pelagic larvae of the Acanthuridae. In assessing the systematic position of the Caproidae as acanthuroid perciforms related to his newly established family Acanthonemidae (for the Eocene *Acanthonemus,* previously placed in the Acanthuridae by Blot 1969), Bannikov (1991) placed the Caprovesposidae in the Acanthuroidei.

In the collections of the Paleontological Institute in Moscow there are now 34 specimens for *Caprovesposus parvus* from the Lower Maikopian deposits of the Lower Oligocene Pshekhsky Horizon in northwestern Caucasus, Russia (31 from the River Belaya, 2 from the River Pshekha, 1 from the River Gumista). There are also two imprints of skeletons, one from the Middle Eocene of Georgia and one from the Middle or Upper Oligocene of Azerbaijan, which Bannikov & Fedotov (1984:710) referred to *Casprovesposus* sp.: the one from Georgia has four or five anal spines and belongs to a different genus discussed below; the one from Azerbaijan is so poorly preserved that its specific identity will probably remain unknown. Additionally, two imperfectly preserved specimens of *Caprovesposus* sp. have been collected from the Lower Miocene (Upper Maikopian) of North Caucasus, Russia (River Belaya), and of Crimea, Ukraine (Kerch Peninsula), while a skeleton of *Caprovesposus* cf. *C. parvus* was found in 1990 in the Upper Eocene Kumsky Horizon (at Gorny Luch on the River Pshekha) of North Caucasus, Russia, as described below.

The illustrated holotype and paratype of *Caprovesposus parvus* (Danilchenko 1960, pl. 9, figs. 2, 3) were both said to be from the River Gumista (Abkhazia). However, the lithology of the matrix of the holotype (the clay is lighter than that in the Lower Maikopian of Abkhazia) indicates that there was a mistake in labeling the holotype. While the paratype is from the River Gumista, the holotype is from the River Belaya (a tributary of the Kuban). Most of the other materials of *C. parvus* also were collected at this River Belaya locality above the settlement of Abadzekhskaya.

Outside of the Caucasus and Crimea, *Caprovesposus* sp. has been reported only from the Middle Miocene of Egypt (Gaudant & Rouchy 1986). However, it probably also occurs in the Oligocene of Iran based on the description and illustration of an incomplete skeleton referred by Arambourg (1967:280, pl. XVII, fig. 3) to "incertae sedis," which we believe is *Caprovesposus*. The report of *Caprovesposus* sp. in the Lower Sarmatian (Upper Miocene) of Rumania (Macarovici 1970) is incorrect, being based on misidentified specimens (Bannikov & Fedotov 1989).

In the course of our joint studies of fossil acanthuroids we have re-examined all of the materials of *Caprovesposus* from Russia and adjacent regions, mostly from the Oligocene but also from the Upper Eocene and Lower Miocene, in the Paleontological Institute (Russian Acad. Sci.) in Moscow. We find that they possess two specializations found only in the Acanthuridae among perciforms: large teeth with highly lobate edges; and a complex locking mechanism of the first two dorsal and anal spines, which rotate over a grooved medial flange of the first basal pterygiophores. These features, plus such other acanthurid specializations as the vacant interneural space between the third and fourth neural spines, are assurance that *Caprovesposus* is an acanthurid (see Tyler et al. 1989 for acanthuroid phylogeny and character analysis). It has the vertically elongate scales and serrated dentary, pelvis, frontal, and mesethmoid (at least at smaller sizes) typical of the acronurus pelagic presettlement stage of extant acanthurids, but differs from them in lacking prominent serrations basally on the second dorsal and anal spines (except in one small specimen) and in the presence in one small specimen of spines on the lower edge of the preopercle, as detailed below.

Description of Oligocene Specimens of *Caprovesposus parvus*

Presented below are the data obtainable on the most salient morphometric and osteological features of the 34 specimens (12.8–29.6 mm SL) of *C. parvus* from the Lower Oligocene Pshekhsky Horizon (Figs. 1, 2, 3a–c).

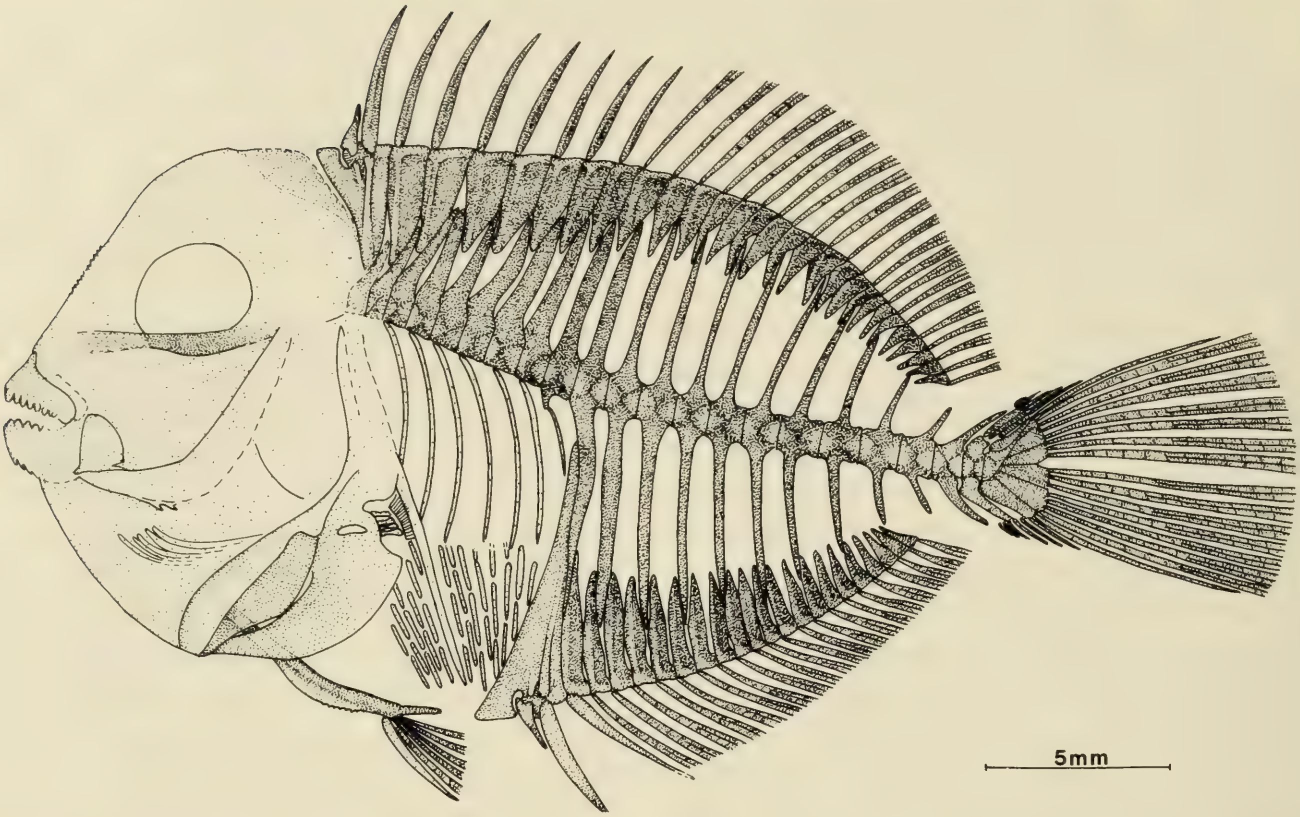

Fig. 1. Reconstruction of *Caprovesposus parvus* Danilchenko, composite based mostly on PIN 1413/645, 26.9 mm SL, with details from other specimens (i.e., preopercular spines based on PIN 1413/666, ca. 16 mm SL, and bone serrations on specimens as listed in text description), all from Lower Oligocene Maikopian deposits (North Caucasus).

Vertebrae 9+13 = 22; caudal skeleton with a parhypural, five separate hypurals, three epurals, a large uroneural, and haemal spines of the penultimate and antipenultimate vertebrae probably autogenous (Fig. 1; see also Bannikov & Fedotov 1984, fig. 1).

Dorsal spines 9, rays 20–22, usually 20. Anal spines 3, rays 20–22 (perhaps 23 in one specimen), usually 20. Each dorsal and anal spine with a prominent groove along its length. First dorsal and anal spines short, with a deep concavity ventromedially where they rotate over a rounded and deeply grooved flange of the first basal pterygiophore, anterior to which flange is a deep indentation (Fig. 2b). First dorsal and anal spines shorter than depicted by Danilchenko (1967:101, fig. 20). Second dorsal spine usually the longest, with the others decreasing only slightly in length posteriorly in the series. Second anal spine usually slightly shorter than the third.

Danilchenko (1960) gave the dorsal rays as 24–26 and the anal rays as 23–24, but we do not find this many rays present either in the type specimens or in the more numerous materials that have become available subsequently. Differences in interpretation of the often poorly preserved posteriormost rays might account for discrepancies of one ray in our respective counts but we do not believe that either the number of basal pterygiophores in the soft dorsal and anal fins or the space available for rays toward the caudal peduncle would allow for more rays than we record.

Caudal fin with 8+8 = 16 principal rays plus five to seven procurrent rays above and below. Number of pectoral rays difficult to interpret but about 14–15 in the five specimens in which the fin is best preserved.

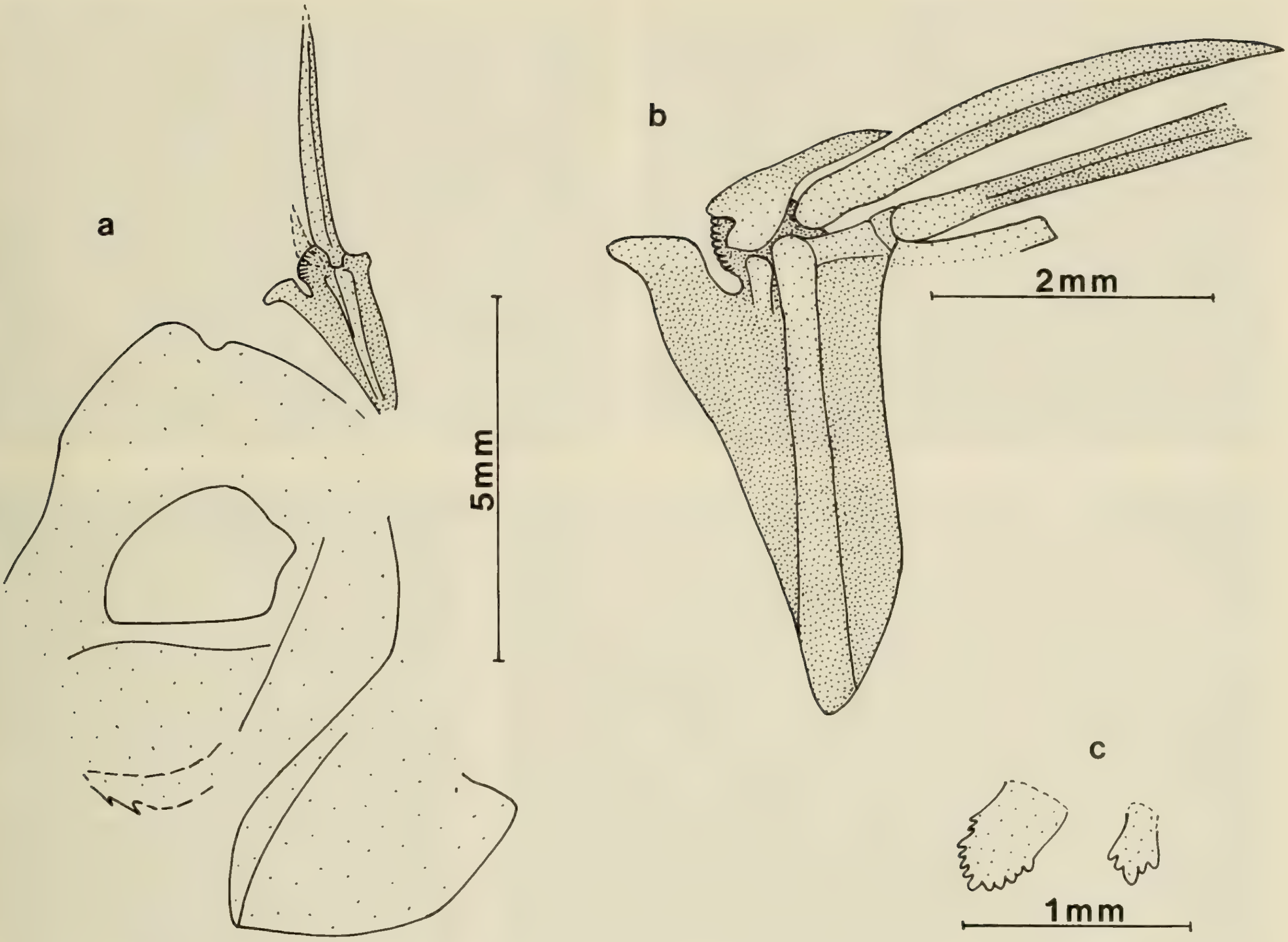

Fig. 2. *Caprovesposus parvus* Danilchenko: a, Note preopercular spines and locking mechanism of first two dorsal spines, PIN 1413/666, ca. 16 mm (incomplete and fragmented into two major pieces, length estimated); b, Detail of the locking mechanism of the dorsal spines (that of the anal fin is comparable to it), PIN 1413/673, 29.6 mm SL; c, Detail of teeth toward medial (the tooth with most lobes) and lateral ends of the tooth bearing edge of the premaxilla, PIN 1413/645, 26.9 mm SL.

Pelvic fin with a strong spine and a questionable number of rays, apparently five in those few specimens in which the rays are most clearly seen (exposed dorsoventrally).

Ventral shaft of first basal pterygiophore of spiny dorsal fin in close contact with occipital region of skull and anterior edge of neural spine of first vertebra. No supraneurals. Vacant interneural space (absence of pterygiophores) between neural spines of third and fourth vertebrae (i.e., two neural spines between third and fourth basal pterygiophores). Pleural ribs present on third to ninth (last) abdominal vertebrae; epipleurals not observed. Coracoid and cleithrum forming a broad basin for muscle attachment; four pectoral actinosts; scapular foramen apparently complete. Pelvis with a prominent posterior process behind level of base of rays; this process and distal end of postcleithrum directed toward anteroventral end of first basal pterygiophore of anal fin but separated from it by a distance about equal to length of one vertebral centrum.

Most of the bones of the head are poorly preserved. The supraoccipital is a low dome without a prominent laterally compressed posterior flange. The branchiostegals are displaced or partially missing in most specimens, but a few specimens provide evidence of five rays, one anteriorly and four

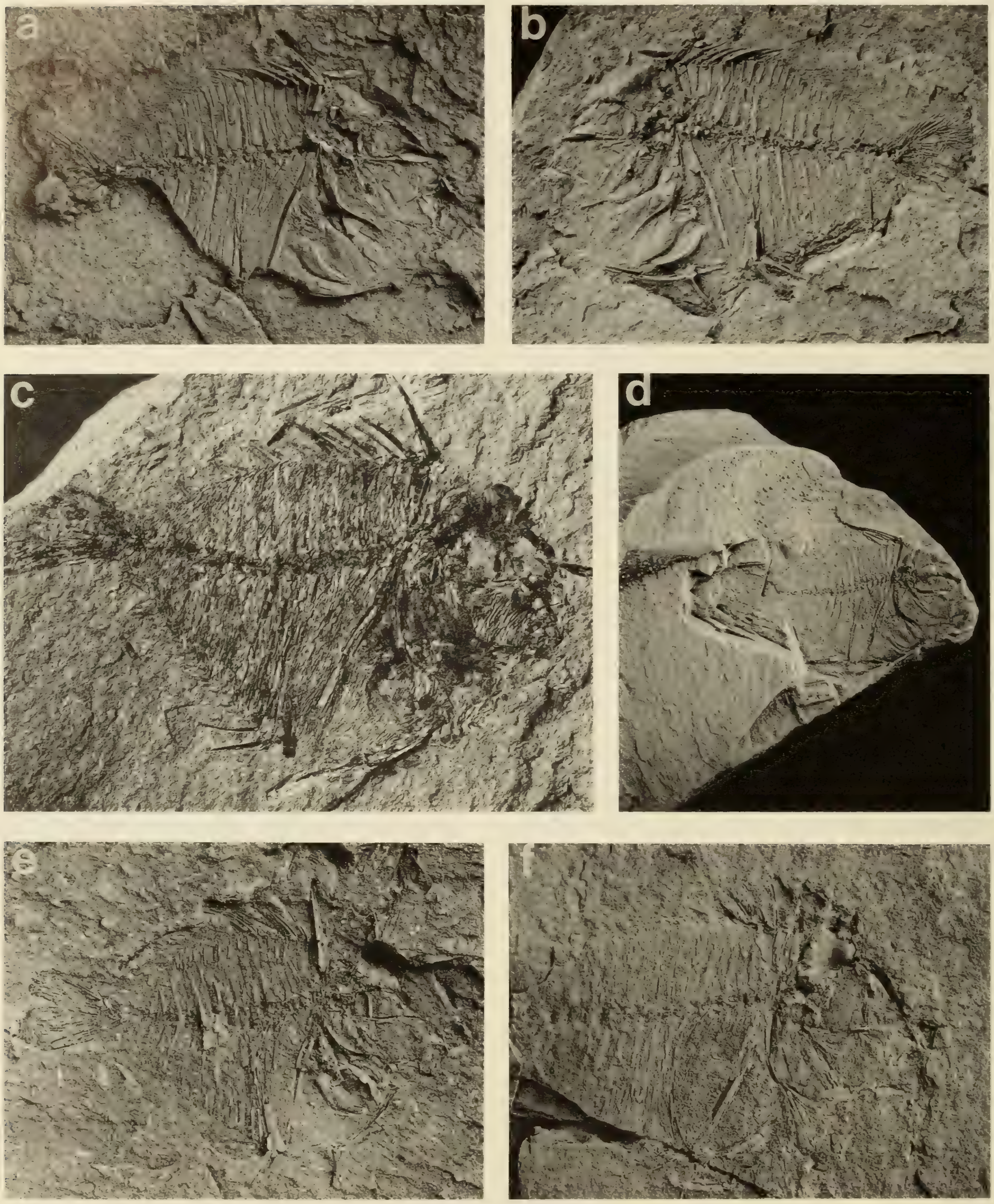

Fig. 3. Acronurus stages of fossil acanthuroid fishes (all at 2× except c at 3×, see text for measurements): a, b, *Caprovesposus parvus* Danilchenko, PIN 1413/667, part and counterpart, Lower Oligocene of North Caucasus, Belaya River; c, *C. parvus,* PIN 484/28, Lower Oligocene of North Caucasus, Gumista River, paratype; d, *Caprovesposus* sp., PIN 3363/102, Lower Miocene of North Caucasus, Belaya River; e, *Caprovesposus* cf. *C. parvus,* PIN 4425/4, Upper Eocene of North Caucasus, Pshekha River; f, Undetermined genus of acanthuroid, PIN 1413/87, Middle Eocene of Georgia, Tbilisi.

posteriorly. The orbit is large, contained a little more than three times in the head length.

The lower edge of the dentary bears prominent serrations in several specimens, and most specimens have at least some evidence of these serrations at a wide range of sizes (14.0–29.6 mm SL). Serrations on other cranial bones are evident in a few of the other specimens, as follows: on the frontal and mesethmoid of PIN 1413/648, ca. 25.5 mm SL; on the frontal or mesethmoid and on the pelvis of PIN 1413/654, ca. 13.8 mm SL, PIN 1413/655, ca. 12.8 mm SL, and PIN 1413/653, 13.6 mm SL; on the frontal of PIN 1413/639, 22.6 mm SL and PIN 1413/676, ca. 23 mm SL; on the frontal or mesethmoid of 1413/669, 23.2 mm SL; and on the pelvis of PIN 1413/643, ca. 19 mm SL. In one of the smaller specimens (PIN 1413/666, ca. 16 mm SL) the posteroventral edge of the preopercle is more intact than in most others and bears two large spines (Fig. 2a). These preopercular spines have not been observed in any of the larger specimens with relatively intact lower edges of this bone and the spines may have been resorbed ontogenetically. In another of the smaller specimens (PIN 1413/653, 13.6 mm SL) minute serrations are present on the second dorsal and anal spines; these serrations apparently were lost with increasing size because we do not find them in any of the other materials.

The teeth are large, few in number (about 6–8 in each premaxilla and about the same in the dentary), and highly lobate (Fig. 2c). The largest teeth, toward the midline, have the largest number of lobes (11–13), while the more lateral teeth are progressively smaller and have the fewest (5).

The scales are vertically elongate, with smooth edges, no surface ornamentation, and rounded distal ends. Although often poorly preserved in their entirety, the deepest scales are about 9–10% SL. In none of the Oligocene specimens do we find evidence of caudal peduncle armature, either as a folding spine or fixed plates.

Measurements as percent of standard length for the better-preserved specimens are as follows: body depth 53–65 (59 average) in 17 specimens; length of head 31–40 (35) in 14; least distance between anterior edge of orbit and profile (approximately medial edge of frontal) 4–6 (5) in 8; length of second dorsal spine (the first long spine) 14–25 (18) in 11; length of spiny dorsal-fin base 22–26 (24) in 11. The smallest specimen measured, 13.6 mm SL, has proportionally the greatest body depth, head length, and second dorsal spine length.

Upper Eocene Specimen of *Caprovesposus* cf. *C. parvus*

The single specimen of *Caprovesposus* from the Upper Eocene of North Caucasus, Russia (PIN 4425/4, 25.9 mm SL, Fig. 3e), differs significantly from the Lower Oligocene specimens of *C. parvus,* although it has such typical features as lobate teeth, vertically elongate scales, locking mechanism of the first two dorsal and anal spines, vacant interneural space between third and fourth neural spines, etc. The Upper Eocene specimen has small serrations along the nasal, a condition we have not found in any Oligocene specimen. It has rather small serrations on the frontal and large serrations on the dentary similar to those in some Oligocene specimens. The distal end of the postcleithrum contacts the anteroventral end of the first anal pterygiophore, while it is more remote from it in the Oligocene (and Lower Miocene, see below) specimens. It has a greater distance between the orbit and the edge of the profile, 7.7% SL, than in the Oligocene specimens, 4–6% SL, although this difference could be due at least in part to distortion. Given these several differences between the Upper Eocene specimen and those of *C. parvus* from the Lower Oligocene, and considering their different geological ages, the Upper Eocene specimen could represent the acronurus of a species different than *C. parvus,* and we refer to it as *Caprovesposus* cf. *C. parvus.*

The Upper Eocene specimen is the only one in which there clearly appears to be the remains of an elongate spine (1.1 mm) on the caudal peduncle along the axis of the vertebral column in the region of the 10th and 11th caudal vertebrae. We interpret this as a folding spine rather than a fixed plate. Whether *C. parvus* from the Lower Oligocene also had a spine on the caudal peduncle (either not preserved in the present specimens or not yet developed—the spine forms only at larger acronurus sizes in extant acanthurids) remains to be determined by additional materials.

Lower Miocene Specimen of *Caprovesposus* sp.

The poorly preserved single specimen of *Caprovesposus* from the Lower Miocene of North Caucasus, Russia (PIN 3363/102, 15.1 mm SL, Fig. 3d), differs slightly from those of *C. parvus* from the Lower Oligocene by a greater distance between the orbit and the profile, 7.3% SL, being almost as distinctive in this measurement as the Upper Eocene specimen. Although we can interpret only a few characters of this poorly preserved specimen, this slight difference along with the difference in geological age leads us to refer to the Lower Miocene specimen as *Caprovesposus* sp.

An incomplete fragment of the middle of the body of another similar specimen (PIN 3974/9) of the same Lower Miocene age but from the Crimea, Ukraine, also is presumed to be *Caprovesposus* sp.

Middle Eocene Specimen (Acanthuroidei *Incertae Sedis*)

A poorly preserved single acronurus-like specimen from the Middle Eocene Dabakhan Formation of Georgia (PIN 1413/87, 31.5 mm SL, Fig. 3f) seems to have the general configuration of *Caprovesposus* and other acanthurids. These features include weak traces of vertically elongate scales, indications that the first dorsal and anal spines were short and had a complex locking mechanism, large second dorsal and anal spines, nine abdominal vertebrae (we cannot determine the number of caudal vertebrae but the size and shape of those we can see are consistent with the 13 of acanthurids), and a vacant interneural space between the third and fourth neural spines; the teeth are not preserved. However, it differs from all known acanthurids, fossil and extant, by having at least four and perhaps five anal spines and in having the posterior process of the pelvis in contact with the anteroventral end of the first anal pterygiophore. It differs from *Caprovesposus* in probably having eight rather than nine dorsal spines and from *C. parvus* in having the ventral postcleithrum almost in contact with the anteroventral end of the first anal pterygiophore, as in the Upper Eocene specimen of *Caprovesposus.*

With at least four anal spines, this acronurus-like specimen cannot be accommodated in any described genus of fossil or extant acanthurid. Because we have only a single poorly preserved specimen for which many critical features are unclear, we simply call attention to it here without further description and refer to it as an undetermined genus of acanthuroid. We note that among acanthuroids four anal spines are found in the primitive Eocene siganid *Ruffoichthys* (Tyler & Sorbini 1991) and in the Eocene acanthonemids (Bannikov 1991). While the extant siganids have the posterior pelvic process and distal end of the postcleithrum in contact or close proximity with the anteroventral end of the first anal pterygiophore, as in the Middle Eocene acronurus-like specimen, the ends of the pelvis and postcleithrum are remote from this pterygiophore in *Ruffoichthys* (and *Acanthonemus*). The Middle Eocene acronurus-like specimen differs from both siganids and acanthonemids by having a much larger number of dorsal- and anal-fin rays in longer based fins, while it differs from presettlement siganids by being acronurus-like, a stage not found in siganids.

Comparison of *Caprovesposus* to Acanthurid Genera

The Oligocene *Caprovesposus parvus* is the acronurus stage of an acanthurid. However, it differs from the acronurus stage of all extant genera in two ways. In *C. parvus* there are no well-developed serrations on the second dorsal and second anal spines (although minute serrations are present on these spines in one small specimen) and none on the pelvic spines. Such serrations are a derived feature of all extant larval acanthuroids (except anal spines absent in luvarids). At least at small sizes (16 mm SL), *C. parvus* has two large spiny processes at the posteroventral edge of the preopercle, while a smooth preopercular edge (except for minute spines lost by 5 mm SL or less) is a derived feature of all larval acanthurids. Large preopercular spines like those of *C. parvus* also characterize the larvae of siganids, zanclids, luvarids, and the outgroups among the squamipinnes and many percoids, although these spines are lost by about 9 mm SL in zanclids and are reduced in size by 35 mm SL in luvarids. The serrations found on the dentary, frontal, and pelvis of *C. parvus* and also on the nasal and pelvis of *C.* cf. *C. parvus* are synapomorphies of either all acanthuroids (those on the frontal and nasal) or of several families (luvarids, zanclids, acanthurids for those on the dentary, and siganids and acanthurids for those on the pelvis). For analyses of the larval features of extant acanthuroids mentioned above, see Leis & Richards (1984), Johnson & Washington (1987), and Tyler et al. (1989).

We note that among the features used by Bannikov (1991) in assessing the relationships of the Eocene acanthonemids and the fossil and extant caproids with acanthuroids were the presence in both groups of serrations along the crest of the frontal and supraoccipital, on the lower edge of the pelvis in front of the pelvic spine, and on the first or second (if first is reduced in size) dorsal, anal and pelvic spines (unlike the others, the dentary is not serrate in small *Acanthonemus*).

Thus, *C. parvus* retains plesiomorphic conditions of the ornamentation of the dorsal, anal, and pelvic spines (well-developed serrations absent) and the preopercle (spiny processes present) not found in extant acanthurids. Therefore, it cannot be considered the acronurus stage of any extant genus.

There are numerous fossil acanthurids to be considered as the possible adults of the *Caprovesposus* acronurus stage. Blot & Tyler (1991) recognized eight genera and 13 species of acanthurids from the Eocene of Monte Bolca, Italy. Additionally, a single species of acanthurid is known from the Oligocene, *Naseus scombrurus* Arambourg (1967). The only other fossil acanthurid is *Zebrasoma deani* Hussakof (1907), which is of uncertain but perhaps Eocene age and has been referred to *Eonaso* by Blot (1984). Both *Naseus scombrurus* and *Eonaso deani* are similar to the Recent *Naso* in having fixed plates on the caudal peduncle and a low number of dorsal spines (respectively six and five when the short first spine overlooked in the original descriptions is taken into account). Six of the eight genera of Eocene acanthurids described by Blot & Tyler (1991) also have eight or fewer dorsal spines and therefore none of these can be the adults of the nine-spined *Caprovesposus.* There are only two fossil genera with nine dorsal spines, *Proacanthurus* with four species and the monotypic *Metacanthurus.*

Caprovesposus is similar to *Proacanthurus* in many morphometric and meristic features, except for having a deeper body associated with small size. However, *Proacanthurus* is like all other Eocene acanthurids in having a supraneural, which is absent in *Caprovesposus.* In *Proacanthurus* the ventral shaft of the first basal pterygiophore of the spiny dorsal fin is closely associated with the anterior edge of the neural spine of the first vertebra. The shaft in *Proacanthurus* does not seem to make especially close contact with the occipital region of the skull (although the possibility of even small amounts of displacement in the position of the pterygiophore makes interpretation of this feature somewhat uncertain). The shaft in *Caprovesposus* and extant acanthurids is more closely in contact with the skull. These differences, along with that in their geological ages, lead us to believe that while *Caprovesposus* may be closely related to *Proacanthurus,* it probably is not the acronurus stage of that genus.

The other fossil acanthurid with nine dorsal spines is *Metacanthurus,* based on a single poorly preserved small specimen that is only marginally distinct from *Proacanthurus.* The posterodorsal region of the skull and anterior region of the first basal pterygiophore of the spiny dorsal fin are missing so it cannot be determined if a supraneural was present (presumably it was, as in all other Monte Bolca acanthurids) or how close the first dorsal pterygiophore was to the occiput. However, *Metacanthurus* has a strikingly oblique (about 45%) head profile, far less steep than in *Caprovesposus.* The 26 mm SL specimen of *Metacanthurus* is a young juvenile not far removed from the acronurus stage as evidenced by the presence of serrations on what is either the premaxilla or lachrymal. The especially oblique profile of *Metacanthurus* (along with the presumed presence of a supraneural) indicates that it probably is the juvenile of a taxon other than *Caprovesposus.*

In short, the Oligocene *Caprovesposus* probably is not congeneric with the Eocene *Proacanthurus* and *Metacanthurus,* the only other fossil acanthurids with nine dorsal spines.

One other fossil genus, *Gazolaichthys,* from the Eocene of Monte Bolca, included in the acanthuroids by Blot & Tyler (1991) as *incertae sedis,* deserves mention here because it also has nine dorsal spines. *Gazolaichthys* has derived features of both acanthurids and siganids, and differs most notably from *Caprovesposus* by having the vacant interneural space between the fourth and fifth vertebrae, a supraneural, and numerous small teeth with smooth edges.

An acronurus stage has been described by Blot & Tyler (1991) among the well-preserved acanthurids from the Eocene of Monte Bolca. It is similar to *Caprovesposus* in having serrations on the frontal and dentary and a deep body. It differs from *Caprovesposus* in having seven dorsal spines, a supraneural, and serrations on the ascending process of the premaxilla. Based on its meristics, Blot and Tyler believed that it was probably the acronurus stage of one of the two species of the Eocene genus *Eorandallius.*

Conclusion

Caprovesposus is the acronurus stage of an Oligocene acanthurid whose adults have not yet been described.

Material Examined

All specimens are from the Paleontological Institute (PIN), Moscow.

Caprovesposus parvus from the Lower Oligocene of River Belaya, North Caucasus, Russia: PIN 484/27, holotype, in counterpart, 19.2 mm SL; 1413/639, in counterpart, 22.6 mm SL; 1413/640, single plate, 23.2 mm SL; 1413/675, single plate, incomplete skeleton, length of vertebral column 18.5 mm; 1413/642, in counterpart, head absent, length of caudal region of vertebral column 10.5 mm; 1413/641, in counterpart, upper part of body absent, length of caudal region of vertebral column ca. 12.2 mm; 1413/649, in counterpart, ca. 22.6 mm SL; 1413/672, in counterpart, posterior part of body only, length of caudal region of vertebral column ca. 12.0 mm; 1413/665, in counterpart, 21.0 mm SL; 1413/643, in counterpart, ca. 19 mm SL; 1413/676, in counterpart, ca. 23 mm SL; 1413/663, in counterpart, head absent, length of caudal region of vertebral column 14.0 mm; 1413/656, in counterpart, incomplete and partially disarticulated, length of middle 13 vertebrae 10.1 mm; 1413/653, single plate, 13.6 mm SL; 1413/659, single plate, incomplete, length of middle 17 vertebrae 13.6 mm; 1413/644, single plate, ca. 25.2 mm SL; 1413/660, single plate, incomplete anteroventrally, length of vertebral column 11.6 mm; 1413/669, single plate, 23.2 mm SL; 1413/657, single plate, head and fins partially disarticulated, length of vertebral column ca. 13 mm; 1413/655, single plate, head and fins partially disarticulated, ca. 12.8 mm SL; 1413/651, single plate, 21.7 mm SL; 1413/664, single plate, head and anterior part of body of relatively large specimen, length of head and abdominal region of vertebral column 16.0 mm; 1413/654, single plate, specimen partially distorted posteriorly, ca. 13.8 mm SL; 1413/650, single plate, fragment of relatively large specimen, length of middle 7 vertebrae 6.6 mm; 1413/647, single plate, head partially disarticulated, ca. 25.9 mm SL; 1413/648, single plate, head partially disarticulated, ca. 25.5 mm SL; 1413/658, single plate, ventral region absent, ca. 26.8 mm SL; 1413/666, single plate, partially disarticulated, ca. 16 mm SL; 1413/667, in counterpart, 26.4 mm SL; 1413/645, single plate, 26.9 mm SL; 1413/673, single plate, 29.6 mm SL.

Caprovesposus parvus from the Lower Oligocene of River Pshekha, North Caucasus, Russia: 1413/671, in counterpart, caudal fin and supports absent, ca. 21 mm SL; 1413/661, head in single plate, body in counterpart, small specimen with caudal region of vertebral column 5.5 mm.

Caprovesposus parvus from the Lower Oligocene of River Gumista, North Caucasus, Russia: 484/28, paratype, in counterpart, 23.0 mm SL.

Caprovesposus sp. from the Upper (Middle?) Oligocene of River Sumgait, Azerbaijan: 2180/264, single plate, poorly preserved, 22.1 mm SL.

Caprovesposus sp. from the Lower Miocene of River Belaya, North Caucasus, Russia: 3363/102, single plate, snout incomplete anteriorly, 15.1 mm SL.

Caprovesposus sp. from the Lower Miocene of Kerch Peninsula, Crimea, Ukraine: 3974/9, single plate, incomplete, length of middle 9 vertebrae 6.5 mm.

Caprovesposus cf. *C. parvus* from the Upper Eocene of River Pshekha, North Caucasus, Russia: 4425/4, in counterpart, 25.9 mm SL.

Acanthuroidei *incertae sedis* from the Middle Eocene of Tbilisi, Georgia: 1413/87, single plate, 31.5 mm SL.

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A NEW LIZARD OF THE GENUS *ARTHROSAURA* (TEIIDAE) FROM SOUTHERN VENEZUELA

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Abstract.—*Arthrosaura synaptolepis,* new species, is a microteiid lizard from highland localities (1200–1450 m) on Cerro de la Neblina and Pico Tamacuari in the borderland between Venezuela and Brazil. It differs from all other *Arthrosaura* in lacking prefrontal scales and in having two (vs. three) pairs of genials. These diagnostic characters seem to have arisen from fusions of a more primitive set of head plates. Other morphological characters and their distributions on the Guayana Highlands suggest that *Arthrosaura synaptolepis* may be the sister species of *A. tyleri.*

Resumen.—El lagarto *Arthrosaura synaptolepis,* especie nueva, es un microtéido de localidades altas (1200–1450 m) en el Cerro de la Neblina y el Pico Tamacuari en la frontera entre Venezuela y Brasil. Se distingue de todas las demás especies de *Arthrosaura* por carecer de escamas prefrontales y en que tiene dos (en vez de tres) pares de geniales. Estos atributos diagnósticos parecen haberse derivado por fusiones de conjuntos más primitivos de escamas de la cabeza. Otras características morfológicas, y distribucionales incluyendo algunos tepuis venezolanos, sugieren que *Arthrosaura synaptolepis* es la especie hermana de *A. tyleri.*

Recent explorations in the broken highlands of extreme southern Venezuela revealed the existence of many undescribed species in the montane herpetofaunas (McDiarmid & Paolillo 1988, Donnelly & Myers pers. obs.). The present description is of a small lizard discovered at disjunct localities on the Brazilian border during expeditions sponsored by the Venezuelan Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales (FUDECI).

Materials and Methods

The three specimens in the type series of the new species are shared among the collections of the American Museum of Natural History, New York (AMNH), the Museo Biología of the Instituto de Zoología Tropical, Universidad Central de Venezuela, Caracas (MBUCV), and the National Museum of Natural History, Washington, D.C. (USNM). The specimen to be catalogued at MBUCV is parenthetically identified by a USNM catalog number at first citation.

We also examined the following congeneric specimens: *Arthrosaura kockii.* Surinam: Brokopondo: Brownsberg, Mazaroni Plateau, 500 m, AMNH 119400–05. *Arthrosaura reticulata.* Venezuela: Amazonas: Neblina Base Camp on Río Mawarinuma, 140 m (00°50′N, 66°10′W), AMNH 133664–65, USNM 317874–79. *Arthrosaura tyleri.* Venezuela: Amazonas: Cerro Duida, 2164 m, AMNH 36643–45 (type series of *Pantodactylus tyleri*). Bolívar: Meseta de Jaua, 1750–1800 m, USNM 317880. *Arthrosaura versteegii.* Surinam: Brokopondo: 65 km (airline) SSE Paramaribo, 80 m, AMNH 108772, 108774.

Scale lengths were measured to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope. Measurements to the nearest 0.1 mm were taken with digital calipers of: snout to vent length (SVL), straight line distance from tip of snout to vent; head length (HL), tip of snout to posterior margin of tympanum; maximum head width; maximum head depth; body length (BL), axilla to groin from posterior margin of arm to anterior margin of the leg; forelimb length, from axilla to tip of fourth finger; hind limb length, from groin to tip of fourth toe; and tail length, from vent to tip of tail (regenerated portion separated by + sign).

Arthrosaura synaptolepis, new species

Figs. 1, 2A, 3, 5A, B

Holotype.—USNM 317882 (field no. RWM 18167), an adult male collected by Alfred L. Gardner, 27 Feb 1985, at Camp XI, about 6.2 km NNE Pico da Neblina, 1400–1450 m, Cerro de la Neblina, Amazonas, Venezuela (00°51′45″N, 65°58′52″W).

Paratypes.—MBUCV [formerly USNM 317881 (field no. FGT 3238)], a female collected by Fred G. Thompson, 14 Apr 1984, Camp V, about 2 km NNW Pico da Neblina, 1250 m, Cerro de la Neblina, Amazonas, Venezuela (00°49′10″N, 66°00′02″W). AMNH 134195 (field no. CWM 18768), a female collected by C. W. Myers, 11–17 Mar 1989, at the north base of Pico Tamacuari, 1200–1260 m, in the Sierra Tapirapecó, Amazonas, Venezuela (01°13′N, 64°42′W).

Etymology.—The species name, a noun in apposition, is derived from the Greek *synaptos* (joined together) + *lepis* (scale) in allusion to the apparent fusions that gave rise to a reduced number of head plates in this lizard.

Diagnosis.—A small highland species of *Arthrosaura* that differs from all others in lacking prefrontals and in having two pairs rather than three pairs of genials. See Intrageneric Comparisons for additional differences between *Arthrosaura synaptolepis* and the four other currently recognized species (*kockii, reticulata, tyleri, versteegii*).

Description of type series.—The series comprises the male holotype (51 mm SVL) and two female paratypes (45–46 mm SVL); see Table 1 for measurements. Head length 19–22% SVL, 1.3–1.6 times longer than wide, 1.3–1.7 times wider than high. Neck as wide as head and anterior body. Body cylindrical, slightly depressed. Complete tail 2.0 times SVL in AMNH 134195, squarish in cross section at base, tapering toward tip. Limbs pentadactyl, all digits with terminal claws. Forelimbs 21–23% SVL, hind limbs 34–35% SVL; adpressed limbs overlapping slightly (1–2 lateral scales). Tongue lanceolate, covered with imbricate scale-like papillae arranged in oblique rows, tip bifid, smooth; 4/4 oblique infralingual plicae. Anterior teeth conical; posterior teeth laterally compressed, bicuspid or tricuspid.

Head relatively short, depressed; snout rounded (Fig. 1). Rostral wider than deep, visible from above, laterally in contact with nasal and first supralabial, dorsally in contact with frontonasal. Frontonasal hexagonal with concave posterior border, separating nasals. Frontal pentagonal, longer than wide. Two pentagonal frontoparietals with a short median suture. Interparietal pentagonal, longer than wide, with a straight posterior margin. Parietals longer than wide, wider than interparietal. Five rectangular occipitals (postparietals), tending to be shorter and wider than dorsal neck scales; lateralmost occipitals smaller than subequal central scales in Neblina specimens, median scale smallest and others subequal in AMNH paratype (Fig. 1). Three supraoculars in direct contact with superciliaries, anteriormost smallest, posteriormost slightly larger or equal to central scale. Nostril in ventral half of undivided nasal. Loreal longer than wide, separated from second supralabial by preocular. Preocular triangular, small, in contact with loreal anteriorly, first subocular posteriorly, and second supralabial ventrally. Three suboculars; suture between second and third centered beneath pupil. Two or three postoculars (2/2 in holotype, 3/2 in MBUCV paratype, 3/3 in AMNH paratype). Four or five superciliaries (5/5 in holotype and MBUCV paratype, 4/4 in AMNH paratype), anteriormost large, second and third thin and elongate, posteriormost small and round. Temporal region with smooth, pentagonal, juxtaposed scales in four rows; 3–5 temporals between postocular series and scales bordering ear opening (3/4 in holotype, 4/4 in MBUCV paratype, 5/5 in AMNH paratype). Ear opening higher than wide, rounded anterior margin bordered by small scales projecting posteriorly; posterior margin straight; auditory meatus shallow, tympanum visible. Six supralabials, fourth under eye, fifth largest, second smallest; one elongate scale between supralabial series and ear opening. Lower eyelid with a translucent disk of 2–3 large, nonpigmented scales (2/2 in holotype, 3/2 in MBUCV paratype, 3/2 in AMNH paratype); one row of small scales between the superciliary series and the upper eyelid ciliaries. Pupil round.

Mental with slightly concave posterior margin. Postmental large, heptagonal, wider than long, in lateral contact with infralabials 1 and 2. Two pairs of genials (large paired scales posterior to the postmental, lying between the infralabials and generally in contact with each other medially); anterior pair longest and in contact with infralabials 2 and 3; posterior pair in contact with infralabials 3 and 4, in medial contact in holotype and MBUCV paratype but separated by one scale in AMNH paratype. A pair of enlarged postgenials or pregulars in posterior contact with second pair of genials; the paired pregulars medially separated by a cluster of 4–8 scales (4 in holotype, 7 in AMNH paratype, 8 in MBUCV paratype) and anterolaterally well separated from last infralabial. Five infralabials.

Head scales smooth, with numerous pores, which tend to be most concentrated around margins of head plates and temporal scales.

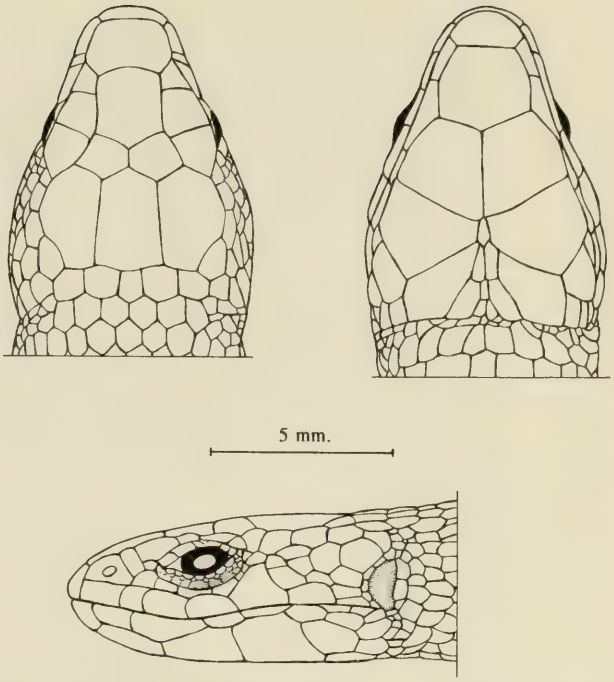

Fig. 1. Head of *Arthrosaura synaptolepis* in dorsal, ventral, and lateral views (AMNH 134195, female paratype). Translucent disk scales of lower eyelid are shaded gray.

Five or six transverse rows of gulars between pregulars and collar scales (6 in holotype and AMNH paratype, 5 in MBUCV paratype); gular scale size increases and the gular number decreases posteriorly; gulars imbricate, with rounded posterior margins. Collar row with five scales, longer than wide, the lateral scales smallest. Two or three rows of small scales hidden by posterior margin of collar; scales largest in posterior row, less than one-third length of ventral scales. Side of neck anterior to arm with medium-sized, rounded, juxtaposed scales; axillary region with smaller, round juxtaposed scales.

Dorsal and lateral body scales of equal size; pentagonal (appearing hexagonal owing to imbrication), weakly keeled, imbricate, mucronate, with pores on posterior margins; scale length more than twice scale width, in 28–30 transverse rows from occipitals to posterior margin of leg (29 in holotype, 28 in MBUCV paratype, 30 in AMNH paratype); transverse rows parallel;

no middorsal discontinuity in scale size. Ventrals smooth, rectangular, imbricate with rounded posterior margins; in eight longitudinal and 18–20 transverse rows (18 in holotype and MBUCV paratype, 20 in AMNH paratype). Scales around midbody 35–36 (35 in holotype, 36 in paratypes).

Six preanal scales, including one large anterior scale and a row of five posterior scales just anterior to vent. Male holotype with 2/2 preanal pores and 5/4 femoral pores, each pore surrounded by three scales; pores absent in females.

Dorsal and lateral caudal scales pentagonal, weakly keeled, mucronate, imbricate, in transverse rows. Subcaudals smooth, imbricate, with rounded posterior margins; larger than dorsal and lateral caudal scales. Eighty-three whorls of caudal scales in the AMNH paratype; ratio of number of whorls to mm of tail length 0.92–1.04 (0.97 in holotype).

Anterodorsal surface of arm with large, smooth, rhomboidal, imbricate scales that are more than twice the width of dorsal body scales. Posteroventral surface of arm with small, round, juxtaposed scales. Anteroventral surfaces of leg with large, smooth, rhomboidal, imbricate scales that are more than twice the width of dorsal body scales. Posterior leg surfaces and ankle with small, round, imbricate scales. Palms and soles with small, round, juxtaposed scales that are not thickened or raised.

Subdigital lamellae as follows (Roman numerals = digits, Arabic numbers = subdigital lamellae on left/right feet); only longest (4th) digits show variation (separate counts given for holotype, MBUCV, and AMNH paratypes, respectively): Forefoot, I 2/2 II 7/7 III 11/10 IV 11/10, 12/13, 11/11 V 7/7. Hind foot, I 3/3 II 8/8 III 11/11 IV 16/16, 18/17, 15/15 V 10/9.

Coloration in life.—Dorsal surfaces brown (Neblina male holotype and Tamacuari female) or grayish black (Neblina female), and dorsal body scales with darker brown to blackish anterior and posterior margins. A discontinuous yellowish tan dorsolateral line extends posteriorly from above shoulder onto tail base of Neblina male; this pale dorsolateral line (color not noted) distinct only anteriorly and posteriorly in Neblina female, absent in Tamacuari female. Sides of body with several (2–6 per transverse scale row) pale spots on posterior halves of lateral scales (yellowish tan in male, not recorded from living females); these pale spots aligned in Neblina specimens as one (female) or two (male) discontinuous lateral-ventrolateral lines. Pale labial spots white (holotype) or tan (Tamacuari) in life. Tendency for a few light spots (living color not noted) on posterior thigh surfaces.

The ventral surfaces of body, limbs, and tail of the Neblina male were bright red-orange with a paler V-shaped mark outlining lower jaw. Similarly, the ventral surfaces of the Tamacuari female were entirely orange, which was darkest and brightest beneath hind limbs and tail. In contrast, the Neblina female had a light gray throat, pale yellow venter, yellowish gray beneath forelimbs, yellowish brown beneath hind limbs, and bright red beneath proximal third of tail. Iris dark brown.

In preservative, the sides of the body are perceived as being darker in the male than in the females (Fig. 2): the flanks of the male are much darker brown than the dorsum, whereas the flanks of the females are about the same (Neblina) or only slightly darker (Tamacuari) than the dorsum. The ventral surfaces turned pale tan in preservative; dark brown flecking is on the lateral margins of the chin shields and gulars; palms and soles are brown; tail tip of Tamacuari specimen is dark brown.

Hemipenis.—The genitalia of the holotype were everted in the field and the left organ was subsequently removed for study and illustration (Fig. 3). The hemipenis is bilobed; the lobes are short and irregularly flattened terminally. The shallow sulcus

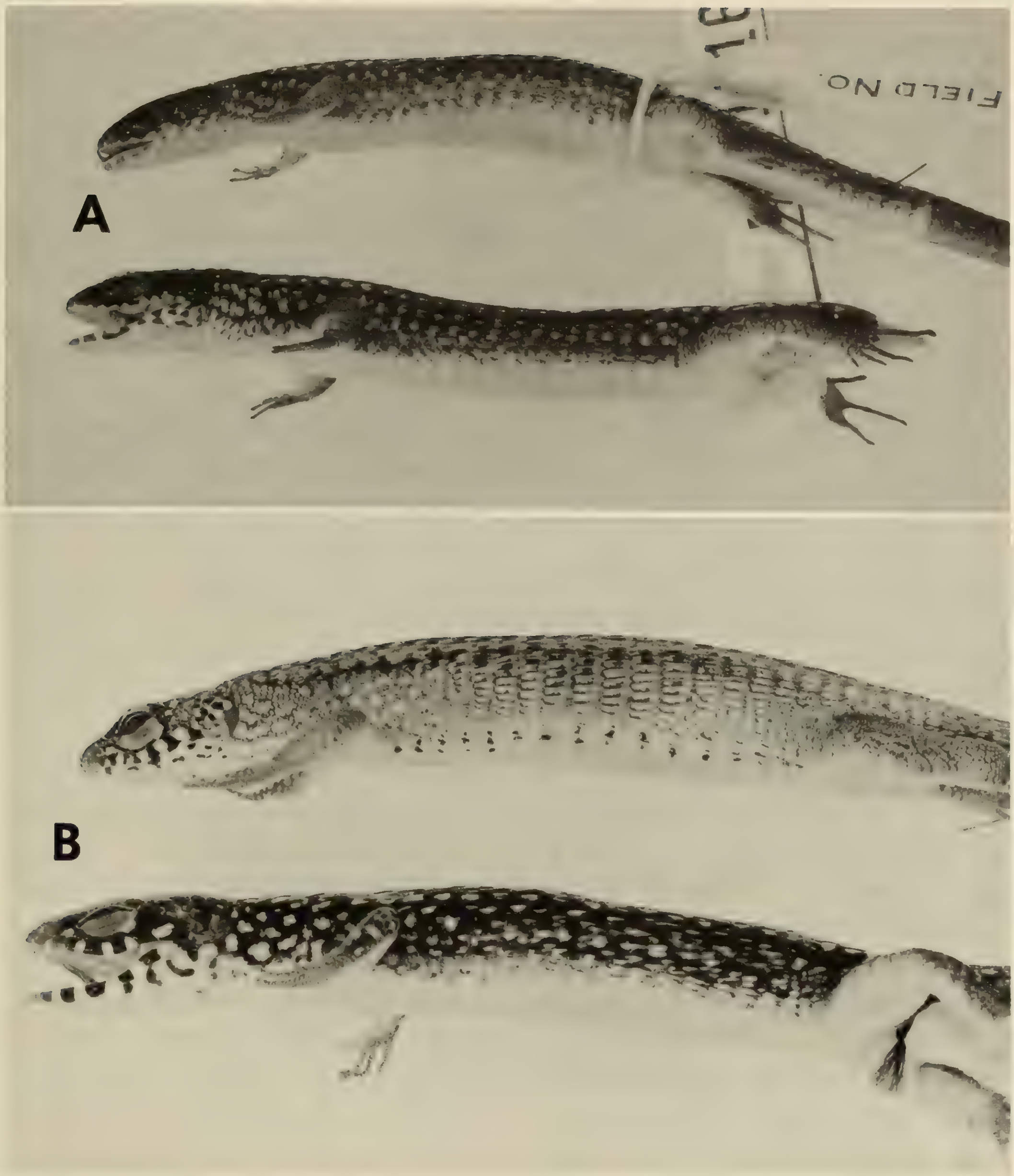

Fig. 2. Lateral views showing sexual dichromatism in (A) *Arthrosaura synaptolepis* (MBUCV female paratype and male holotype) and (B) *A. reticulata* (USNM 317877, female, and AMNH 133665, male), from 1250–1450 m and 140 m (respectively) at Cerro de la Neblina, all × 1. Males (lower specimen of each pair) tend to have darker sides than females, which is most pronounced in *A. reticulata.*

spermaticus runs a medial course to bifurcate at a pronounced elevation of tissue in the crotch of the organ; the sulcus branches extend centripetally towards the apices of the lobes, but the branches are broad, shallow, and poorly defined. Transversely aligned plicae arise on either side of the midline of the asulcate surface and extend around to the sulcate surface, terminating well short of the sulcus spermaticus. The plicae comprise myriad microscopic, calcified spinules, but some spinules on the sides of the organ are larger than others (Fig. 3).

Distribution and habitat.—Arthrosaura synaptolepis is known from only two highland (1200–1450 m) localities, Cerro de la Neblina and Cerro Tamacuari, in the borderland between Venezuela and Brazil. Cerro de la Neblina is an immense tepui (table

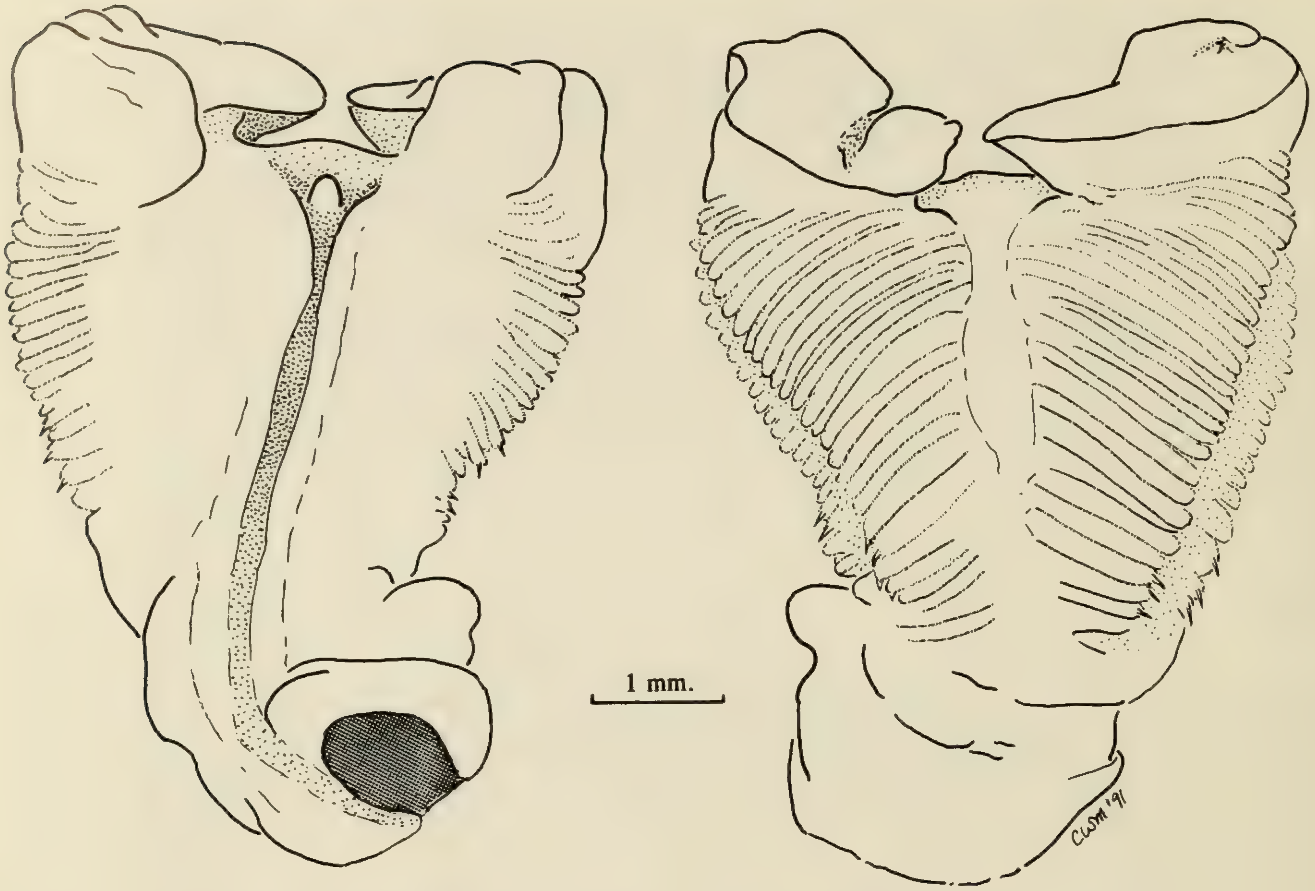

Fig. 3. Everted hemipenis of *Arthrosaura synaptolepis.* Left organ of the holotype.

mountain) that is nearly split by a great canyon. Cerro Tamacuari is not a tepui, although probably a remnant of the same ancient highland. The prominent peaks on these two mountains are on the international border; Pico Tamacuari is about 150 km ENE of Pico da Neblina.

The male holotype was collected about 1500 h along a trail through a dense patch of pitcher plants of the genus *Heliamphora.* The other Neblina specimen was crawling in leaf litter on the forest floor in camp at 1000 h. The Tamacuari specimen was collected on the forest floor by day, on a slope above a rocky stream.

Intrageneric Comparisons

Cunha (1967), whose arrangement was followed by Peters & Donoso-Barros (1970), recognized four species in the genus *Arthrosaura*: *A. amapaensis* Cunha,[1] *A. kockii* (Van Lidth de Jeude), *A. reticulata* (O'Shaughnessy), and *A. versteegii* Van Lidth de Jeude. Following Brongersma (1935), Hoogmoed (1973) treated *A. versteegii* as a subspecies of *A. reticulata* and placed *A. amapaensis* in the synonymy of *A. reticulata versteegii.* Recently, however, Hoogmoed & Avila Pires (pers. comm.) decided to remove *A. versteegii* and *A.* [=*Pantodactylus*] *tyleri* (placed in synonymy by Cunha [1967]) from the synonymy of *A. reticulata.* Based on the American Museum types, we had independently reached the same conclusion on the validity of *A. tyleri,* and we also concur with Hoogmoed & Avila Pires' proposed resurrection of *A. versteegii.* In their yet unpublished manuscript, Hoogmoed & Avila Pires (pers. comm.) provide a historical review and detailed accounts for the species of *Arthrosaura* with three supraoculars (*A. reticulata, A. tyleri,* and *A. versteegii*).

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[1] Authors have followed Cunha's incorrect use of the neuter ending (*amapaense*) for this species name (described in *Arthrosaura,* feminine).

Following, we compare the new species (first value in parentheses) with the four other species of *Arthrosaura* now recognized (second value in parentheses).

Arthrosaura synaptolepis differs from *A. kockii* in the number of supraoculars (3 vs. 4), size, morphology, and number of temporal scales (large and smooth in 4 rows vs. small and keeled in 8 rows), size and shape of lateral neck scales (moderate and round vs. small and granular), degree of keeling of dorsal scales (weakly vs. strongly keeled), presence or absence of keels on dorsal limb scales (smooth vs. keeled), color pattern (no middorsal light stripe vs. middorsal light stripe present), and amount of overlap between adpressed limbs (slight, 1–2 lateral scales vs. substantial, 6+ scales). *Arthrosaura kockii* usually has a proportionately longer head than *A. synaptolepis* (based on data presented for *A. kockii* by Hoogmoed 1973: table 14 [excluding data for RMNH 15226, for which HL seems too small for the given SVL]): Ratio of head length to SVL in *A. synaptolepis* is 0.19–0.22 (0.206 ± 0.015, $n = 3$); HL/SVL in *A. kockii* is 0.20–0.30 (0.266 ± 0.019, $n = 42$). See Table 2 for differences in ratios and selected scale counts among *A. synaptolepis* and the remaining three species of *Arthrosaura* (*reticulata, tyleri,* and *versteegii*)—all characterized by three supraoculars.

Arthrosaura synaptolepis differs from *A. versteegii* in having fewer and larger temporals (4 rows vs. 6–7 rows), size of lateral neck scales (moderate vs. small), size of scales in axilla and groin (small vs. granular), and morphology of the subcaudal scales (pentagonal and imbricate vs. rectangular and juxtaposed).

Table 1.—Measurements for the type series of *Arthrosaura synaptolepis.*

Character	Holotype male	MBUCV paratype female	AMNH paratype female
Snout–vent length	51.0	45.4	46.1
Tail length	9.2 + 4.2	19.3 + 38.7	90.5
Head length	10.8	9.9	8.7
Head width	6.6	6.0	6.7
Head depth	5.2	4.0	4.0
Body length	26.3	22.5	23.7
Forelimb length	11.6	10.0	9.5
Hind limb length	17.7	15.3	15.8

Arthrosaura synaptolepis was compared with several specimens of *A. reticulata* collected at the base of Cerro de la Neblina, a sample that agrees with the account of *reticulata* being prepared by Hoogmoed & Avila Pires (pers. comm.). *Arthrosaura synaptolepis* differs from these specimens in the number and size of temporal scales (4 rows of large scales vs. 6–7 rows of small scales), size of lateral neck scales (moderate vs. small), size of scales in axilla and groin (small vs. granular), degree of keeling of dorsal body scales (weakly vs. moderately keeled), amount of overlap between adpressed limbs (slight, 1–2 lateral body scales vs. moderate to substantial, 3–6 scales), and details of pigmentation (dorsal body scales with dark margins vs. dorsal scales irregularly flecked with black). The apparent common tendency of males to have darker flanks and more distinct pale lateral spots on flanks and tails than females is more strongly pronounced in *reticulata* than in *synaptolepis* (Fig. 2).

Arthrosaura synaptolepis differs from *A. tyleri,* the other tepui species, in degree of keeling of dorsal body scales (weakly vs. strongly keeled), shape of median subcaudal scales (pointed vs. rounded posterior margins), ventral pigmentation (immaculate ventrals vs. heavily pigmented ventrals, see Fig. 4), and amount of overlap of adpressed limbs (slight, 1–2 lateral body scales vs. moderate, 3–4 scales).

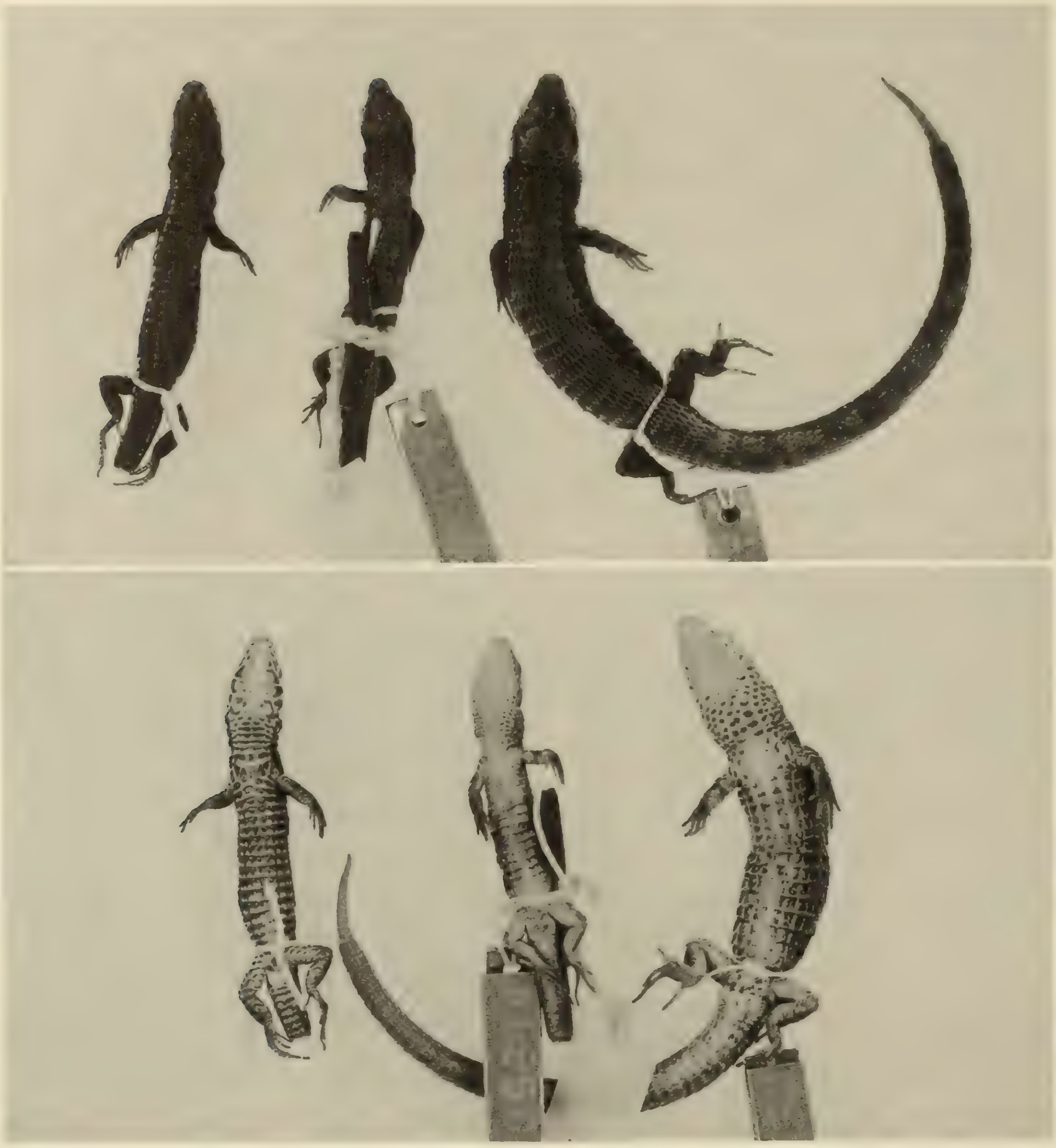

Fig. 4. Dorsal and ventral views of *Arthrosaura tyleri,* ×1. Left to right: USNM 317880, AMNH 36644 (paratype), AMNH 36645 (holotype).

Heretofore, *Arthrosaura tyleri* (Fig. 4) was only known from the type series of three females from over 2000 m elevation on the summit of Cerro Duida. An additional specimen referable to *A. tyleri* is from 1750–1800 m on Meseta de Jaua, roughly 200 km NE of Duida. Although the Jaua specimen has a more rounded snout than the Duida types and an extra genial on the left side, we were unable to otherwise distinguish it morphologically. The Jaua lizard, a male, is darker than the females from Duida and has a series of light dorsolateral spots, but these differences are suggestive of the sexual dichromatism in *A. synaptolepis* and *A. reticulata.*

Ruibal (1952:512), in removing *tyleri* from *Pantodactylus,* suggested that *Arthrosaura tyleri* was related to *A. kockii,* but gave no reasons that exclude a close relationship with one of the species with three supraocular scales. In any case, under the assumption that some unknown portion of the morphological resemblance reflects synapomorphy, *Arthrosaura synaptolepis* may be the closest relative (sister species) of *A. tyleri.* These "tepui species" have fewer midbody scale rows, temporal rows, and sub-

Table 2.—Scale counts and ratios for *Arthrosaura* species with three supraoculars. Values are means ± one standard deviation, range in parentheses.

Character	*A. synaptolepis* ($n = 3$)	*A. tyleri* ($n = 4$)	*A. reticulata* ($n = 8$)	*A. versteegii* ($n = 2$)
Transverse ventrals	18.7 ± 1.15 (18–20)	17.8 ± 0.96 (17–19)	17.0 ± 0.47 (17–20)	16.5 ± 0.71 (16–17)
Transverse dorsals	29.0 ± 1.00 (28–30)	28.5 ± 0.58 (28–29)	28.1 ± 0.99 (27–30)	26.0 ± 0.00 (26)
Scales around midbody	35.7 ± 0.58 (35–36)	34.5 ± 4.12 (31–39)	41.5 ± 1.85 (40–45)	41.0 ± 0.00 (41)
Temporal rows	4.0 ± 0.00 (4)	3.8 ± 1.04 (3–4)	7.3 ± 2.41 (6–7)	6.5 ± 0.58 (6–7)
Palpebrals	2.7 ± 0.82 (2–4)	2.3 ± 0.46 (2–3)	3.6 ± 0.81 (2–5)	2.5 ± 0.58 (2–3)
Subdigital lamellae finger IV	11.3 ± 1.03 (10–13)	11.8 ± 1.17 (10–13)	16.1 ± 1.44 (13–18)	13.0 ± 0.82 (12–14)
Subdigital lamellae toe IV	16.2 ± 1.17 (15–18)	18.8 ± 1.67 (16–21)	20.8 ± 1.57 (17–22)	18.5 ± 0.58 (18–19)
Head length/SVL	0.21 ± 0.004 (0.21–0.22)	0.24 ± 0.013 (0.23–0.25)	0.23 ± 0.014 (0.22–0.26)	0.27 ± 0.019 (0.26–0.29)
Postmental length/HL	0.24 ± 0.024 (0.22–0.27)	0.16 ± 0.029 (0.12–0.19)	0.17 ± 0.008 (0.16–0.18)	0.16 ± 0.005 (0.16–0.17)
Forelimb length/BL	0.43 ± 0.027 (0.40–0.44)	0.51 ± 0.052 (0.46–0.58)	0.57 ± 0.051 (0.47–0.63)	0.55 ± 0.173 (0.42–0.67)
Hind limb length/BL	0.67 ± 0.010 (0.66–0.68)	0.80 ± 0.040 (0.75–0.84)	0.95 ± 0.101 (0.81–1.10)	0.78 ± 0.171 (0.66–0.90)

digital lamellae (Table 2) than lowland *Arthrosaura*. The low number of midbody scale rows is a manifestation of the relatively large dorsal and ventral scales of *Arthrosaura synaptolepis* and *A. tyleri*. Similarly, these are the only species with large smooth scales in the temporal region, accounting for the low number of temporal rows. The tepui species, *Arthrosaura reticulata,* and *A. versteegii* have three supraoculars and differ from *A. kockii* which has four.

The highland localities of the presumed sister species, *Arthrosaura synaptolepis* and *A. tyleri,* are well separated. The two tepuis from which *tyleri* is known are roughly 200 km apart and the two localities for *synaptolepis* are about 150 km from one another. The closest localities (Duida and Tamacuari) between the northern *tyleri* and the southern *synaptolepis* are 250 km apart. Intraspecific variation in the genials of *A. tyleri* helps explain the origin of one of the two autapomorphies of *A. synaptolepis.*

Origin of Diagnostic Characters

Arthrosaura synaptolepis has a relatively shorter head than other species of *Arthrosaura* (Table 2 and Intrageneric Comparisons). This condition is reflected in two characters of *A. synaptolepis* that are unique in the genus: (1) the absence of prefrontal scales and (2) the presence of two rather than three pairs of genials (or, depending on definitions, three rather than four pairs, see below). These seem to be derived features from the fusion of certain head scales. We use the word "fusion" in the sense of phylogenetic transformation and imply nothing about ontogenetic transformation for which no data exist.

Species of *Arthrosaura* typically have a pair of prefrontal scales bounded anteriorly by a large frontonasal, posteriorly by a hexagonal frontal, and laterally by the loreal and the first, or first and second, supraocular scales. In *A. synaptolepis,* the prefrontals are absent; the frontonasal is large and has a medially indented or concave frontal suture in contrast to a medially pointed frontal suture in other species (compare Figs. 1 and 5A [*synaptolepis*] with 5C [*tyleri*] and with figs. 43 [*kockii*] and 45 [*versteegii*] in Hoogmoed, 1973). One of the paratypes has a short (about 0.2 mm) suture extending mediad from each loreal (Fig. 5A); these symmetrical but incomplete sutures appear to be vestiges of the original frontonasal-prefrontals suture (compare Fig. 5C).

Arthrosaura spp. typically have a single postmental followed by three pairs of genials; the usual arrangement of ventral head shields in these lizards is as follows: a postmental is in contact with infralabials 1 and 2 laterally and with the first pair of genials posteriorly; the first pair of genials are in medial contact and in contact with infralabials 2 and 3 laterally; the second pair of genials are in medial contact and in contact with infralabials 3 and 4 laterally; the third pair of genials are separated by 1–3 scales and in contact with infralabials 4 and 5 laterally. A pair of large pregulars or postgenials are in contact anteriorly with the posterior margins of the last pair of genials;[2] the pregulars are separated medially by a cluster of 5–11 small juxtaposed scales that vary in size, shape, and number; the pregulars are well separated from the infralabials. Minor exceptions to this arrangement include an example of *A. reticulata* from the base of Cerro de la Neblina (USNM 317875), whose postmental is in contact with infralabials 1–3 (vs. 1–2) on the right side.

Arthrosaura synaptolepis is the only species in the genus having two rather than three pairs of genials as defined herein. The postmental is much longer in *A. synaptolepis* than in the other species of *Arthrosaura* with three pairs of supraoculars (Table 2); therefore, on topographic grounds we hypothesize that this enlargement seemingly represents the fusion of the postmental with a primitive first pair of genials. Thus, the first pair of genials in *A. synaptolepis* represent the elongate second pair of other species; genial pairs one and two in *A. synaptolepis* are equivalent to pairs two and three of other *Arthrosaura*.

This conclusion is supported by a paratype of *A. tyleri* that has aberrant genials (Fig. 5D). This specimen shows three genials (normal in *Arthrosaura*) only on its right side; on the other side it has only two genials, the condition in all *A. synaptolepis*. A short suture extending mediad into the postmental from the left side, level with the anterior part of the second infralabial, suggests a fusion between the postmental and an anterior genial (Fig. 5D). The USNM specimen assigned to *A. tyleri* from Meseta de Jaua varies from the typical arrangement in another direction: it has four genials on the left side of the head, a condition that does not characterize any known species of *Arthrosaura*.

Some Intergeneric Comparisons

Our suggestion that a lack of prefrontals and a reduced number of genials are derived character states in *Arthrosaura synaptolepis* is based, in part, on ingroup (intrageneric) variation, inasmuch as we are uncertain about the most appropriate outgroups. However, most microteiids have paired prefrontals. Also, three pairs of genials occur in nearly all other genera of microteiids that inhabit the Guiana Shield and this condition seems to be the normal (i.e., presumed primitive) state in most of them (*Alopoglossus, Amapasaurus, Anadia, Ar-*

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[2] We somewhat arbitrarily define genials as large paired plates that are usually in contact with the infralabials laterally (last pair sometimes narrowly separated from labials) and usually in median contact with one another (except last pair often narrowly, or, in some taxa, widely separated). The "pregulars" often are considered as being the fourth (i.e., the posteriormost) pair of genials or "chin shields" in the microteiid literature, but, when present, they vary greatly in size and shape.

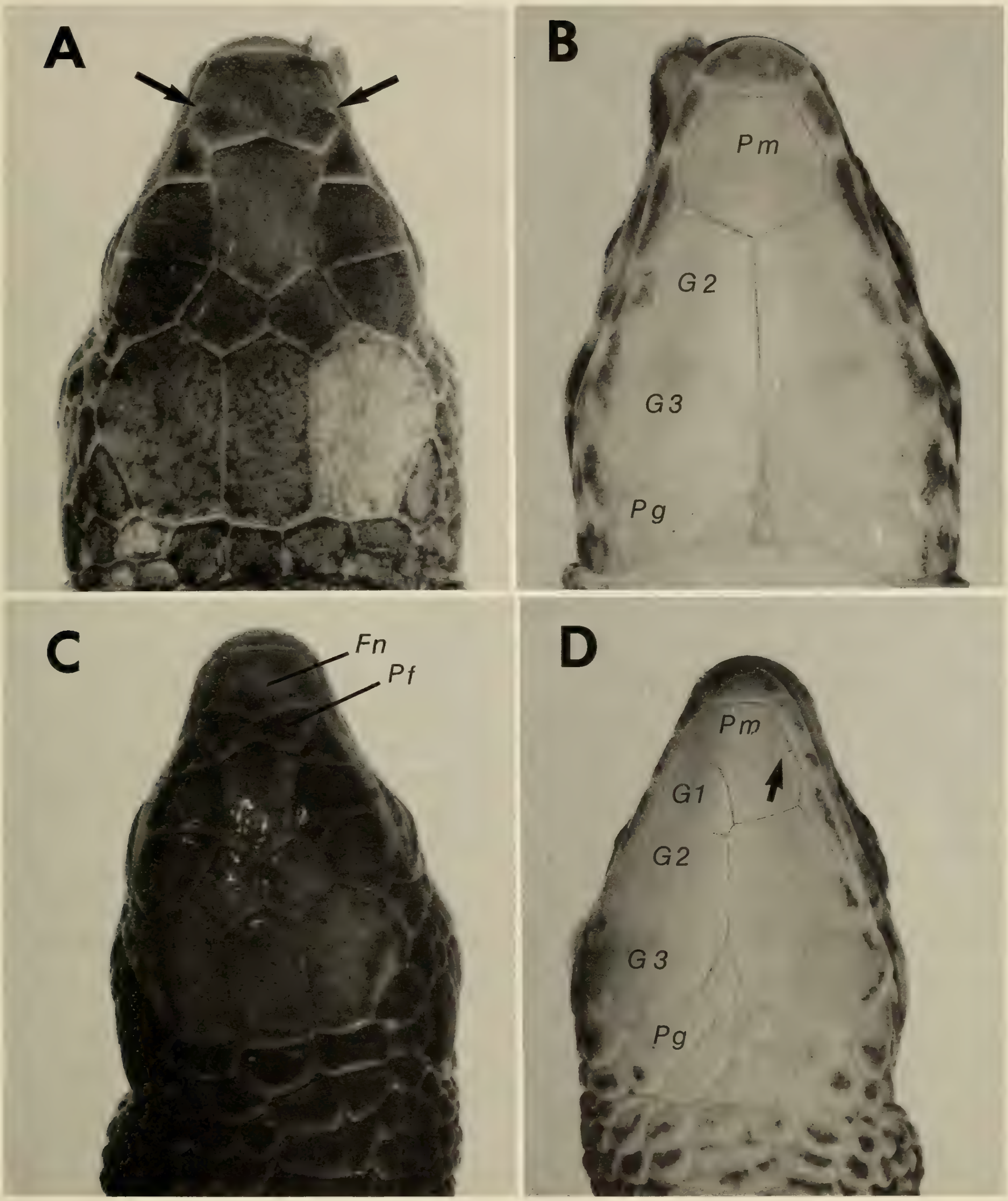

Fig. 5. Dorsal and ventral views of heads of *Arthrosaura synaptolepis* (A–B, MBUCV paratype) and *Arthrosaura tyleri* (C–D, AMNH 36644, paratype), approximately ×8. Abbreviations: Fn, frontonasal; Pf, prefrontal; Pm, postmental; G1–G3, genials 1–3; Pg, large paired pregular. A. An aberrancy in *A. synaptolepis*: Arrows indicate traces of sutures that separate paired prefrontals from the anterior frontonasal in most species of *Arthrosaura* (as in C below). D. An aberrancy in *A. tyleri*: Arrow indicates trace of suture between postmental and first genial on lizard's left side. Failure of G1 to differentiate from the postmental on the left side produces (asymmetrically) the diagnostic condition of *A. synaptolepis* (as in B above).

throsaura, Cercosaura, Euspondylus, Leposoma, Prionodactylus, Ptychoglossus, Riolama, Tretioscincus). The fossorial *Bachia* and the large-scaled *Gymnophthalmus* and *Iphisia* have the size of the ventral head plates much enlarged and the number of plates greatly reduced (with only two pairs of genials in some species of *Gymnophthalmus*); the aquatic or semiaquatic species of *Neusticurus* seem to have either three or four pairs of genials, with the posteriormost pairs widely separated, in correlation with a posterior widening of the head. Presch (1980) placed *Arthrosaura* with several of the above genera (his group 4 = *Arthrosaura, Cercosaura, Neusticurus, Leposoma,* and *Echinosaura*); Presch used osteological data and therefore had to exclude several rare genera, including, for example, *Stenolepis* of northeastern Brazil.

Comparison between *Arthrosaura* and taxa of the Brazilian Shield may eventually prove fruitful in the search for relationships. Boulenger ("1887" [1888]) in fact suggested a relationship between *Arthrosaura* and Brazilian *Heterodactylus* and *Stenolepis.* Both agree with *Arthrosaura synaptolepis* in lacking prefrontals and having only two pairs of genials. They differ from *Arthrosaura* in lacking a collar fold and in having a larger palpebral disk and other details. *Heterodactylus* (in Presch's group 6) furthermore lacks an external ear opening and has very short limbs, with a reduced or absent pollex; distributions of the two species of *Heterodactylus* cluster in southeastern Brazil (see Vanzolini & Ramos 1977).

The monotypic *Stenolepis* from northeastern Brazil (Pernambuco) shows the closest overall resemblance with *Arthrosaura* (based on comparison with one specimen of *Stenolepis ridleyi,* AMNH 131867). If the head-shield resemblances between *Arthrosaura synaptolepis* and *Stenolepis* were homologous, paraphyly of *Arthrosaura* would be suspected. The geographic relationships would not be without precedence, inasmuch as other tepui reptiles may be related to species occurring well south of the Amazon (Donnelly & Myers 1991:46, 49; Frost 1992: 36). However, the postmental is relatively smaller in *Stenolepis* than in *Arthrosaura synaptolepis* and the first of the two pairs of genials is relatively larger, suggesting that the original first pair of genials apparently fused with the second pair (rather than with the postmental as in *A. synaptolepis*). The subtleties of such variation deserve considerably more attention than usually accorded.

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DIAGNOSIS OF A HYBRID ANTBIRD (*PHLEGOPSIS NIGROMACULATA* × *PHLEGOPSIS ERYTHROPTERA*) AND THE RARITY OF HYBRIDIZATION AMONG SUBOSCINES

Gary R. Graves

Abstract.—*Phlegopsis barringeri* Meyer de Schauensee, 1951, is suggested to be a hybrid between *Phlegopsis nigromaculata* and *P. erythroptera*. This represents the first case of hybridity in the large monophyletic assemblage of New World suboscines comprising the woodcreepers, antbirds, ovenbirds, and tapaculos (parvorders Thamnophilida and Furnariida). The rarity of hybridization among suboscines (Suborder Tyranni) may result from the absence of song learning in this assemblage, resulting in vocal stereotypy within populations and the reduction of mate recognition error by females.

Hybridization in birds occurs most frequently in sexually dimorphic species with polygynous breeding systems (Sibley 1957). More than half of all known cases of hybridization in nature occur in four avian families or tribes: Anatidae (ducks, geese, and swans), Phasianidae (grouse and pheasants), Trochilidae (hummingbirds), and Paradisaeini (birds of paradise) (Gray 1958) (taxonomy of Sibley & Monroe 1990). The apparent absence or low frequency of hybridization in other lineages may reflect reality or the failure of biologists to detect it (Graves 1990). Only a few cases of hybridization have been detected among New World suboscines (e.g., Parkes 1961, Short & Burleigh 1965, Tyler & Parkes 1992), which constitute a quarter ($n = 1097$) of all Western Hemisphere species.

Meyer de Schauensee (1951) described a relatively large and spectacular species of antbird, the Argus Bare-eye (*Phlegopsis barringeri*), from a unique specimen collected on the Río Rumiyaco, Department of Nariño, Colombia. Determining whether a unique specimen represents a valid species, a hybrid, or a genetic variant of a previously described species can be a Herculean task. However, because hybrids have no standing in zoological nomenclature, the burden of proof rests upon a taxonomist to reject hybridity before conferring species status (Graves 1990). Meyer de Schauensee compared the specimen of *P. barringeri* with three morphologically similar taxa but failed to address hybridity. That possibility was raised by Willis (1979), who suggested parenthetically that *P. barringeri* was a hybrid between the Black-spotted Bare-eye (*P. nigromaculata*) and Red-winged Bare-eye (*P. erythroptera*), which overlap broadly in western Amazonia from eastern Colombia (Hilty & Brown 1986) south to northern Bolivia (Parker & Remsen 1987).

My analysis of *P. barringeri* confirmed Willis' hunch. The proposed hybrid origin of the specimen (*P. nigromaculata* × *P. erythroptera*) cannot be rejected. Here I present a diagnosis of the hybrid antbird, the first known example of hybridity in the parvorders Thamnophilida and Furnariida (Sibley & Monroe 1990), a monophyletic assemblage representing 131 genera and 560 species of woodcreepers, antbirds, ovenbirds, and tapaculos. I then briefly discuss a correlate of hybridization frequency in suboscines (Suborder Tyranni), the absence of song learning.

Materials and Methods

I compared the holotype of *Phlegopsis barringeri* (adult male, Academy of Natural Sciences Philadelphia (ANSP), No. 162,675) directly with specimens of *P. nigromaculata* and *P. erythroptera* from Ecuador under natural light. A complete description of *P. barringeri,* which will not be repeated here, can be found in Meyer de Schauensee (1951). Series of *Phlegopsis* and nearly all other species of antbirds were examined at the following institutions: American Museum of Natural History; Carnegie Museum of Natural History; Museu Paraense "Emilio Goeldi," Belem; Museum of Natural Science, Louisiana State University (LSUMNS); Museu de Zoologia, Universidade de São Paulo; and the National Museum of Natural History, Smithsonian Institution. Measurements of wing chord, tail length from point of insertion of central rectrices to tip of longest rectrix, tarsus length, hallux (plus claw) length, bill length from anterior edge of nostril, and bill width at anterior edge of nostril were made with digital calipers to the nearest 0.1 mm.

In order to visualize morphological variation in two dimensions, I used principal components analysis of log transformed data. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). P-values of <0.05 were regarded as significant for two-sample t-tests.

Diagnostic assumptions and methods of hybrid diagnosis based on plumage characters and morphology follow Graves (1990). For brevity, I refer to *Phlegopsis barringeri* as a "hybrid" throughout the text.

Results

Potential parental species.—Because the hybrid strongly resembles species of *Phlegopsis* in plumage pattern and color (Fig. 1) and because its collection locality is known, determination of the potential parental species seems straightforward: species of *Phlegopsis,* and related genera, *Myrmoborus, Hypocnemis, Myrmochanes, Sclateria, Percnostola, Myrmeciza, Pithys, Gymnopithys, Myrmornis, Rhegmatorhina,* and *Hylophylax,* that occur in Amazonian forest of Colombia and Ecuador.

Soft part colors.—The hybrid had bare reddish orbital skin (now faded), an apomorphic character of *Phlegopsis* among the Thamnophilida. The size of the orbital patch in the hybrid is intermediate between that of *P. nigromaculata* (larger) and *P. erythroptera* (smaller). This character alone suggests that the two species of *Phlegopsis* were the hybrid's parents. Other "bare-eyed" antbirds have smaller patches of bluish-gray or bluish-white orbital skin in life, which fades to gray in specimens. Hybrids between a species of *Phlegopsis* and a species from another genus would probably, although not certainly, have a small orbital patch with traces of melanization (gray in dried skin).

Plumage characters.—Because the hybrid was male, the plumage diagnosis focused on aspects of male plumage. Meyer de Schauensee (1951:3) noted "this new species combines in some ways characters found in both *P. nigro-maculata* and *P. erythroptera,* and has others not found in either." A careful examination of the hybrid confirms his observation (Fig. 1). No combination of potential parental species, except *Phlegopsis nigromaculata* and *P. erythroptera,* could have produced the distinctive characters of the hybrid: (1) unmarked glossy black head, throat, and breast; (2) brown mantle with contrasting spots; and (3) black and rufous-cinnamon remiges, rectrices, and upper- and undertail coverts. Significantly, the hybrid lacks any trace of pale markings on the head, throat, and breast, or an interscapular patch (found in one or more species of *Myrmoborus, Hypocnemis, Myrmochanes, Myrmeciza, Myrmornis,* and *Hylophylax*). Most elements of the hybrid's plumage pattern and color are easily identified as intermediate character states or mosaics of characters of *Phlegopsis nigromaculata* and *P. erythroptera.* However, the buff and rufous

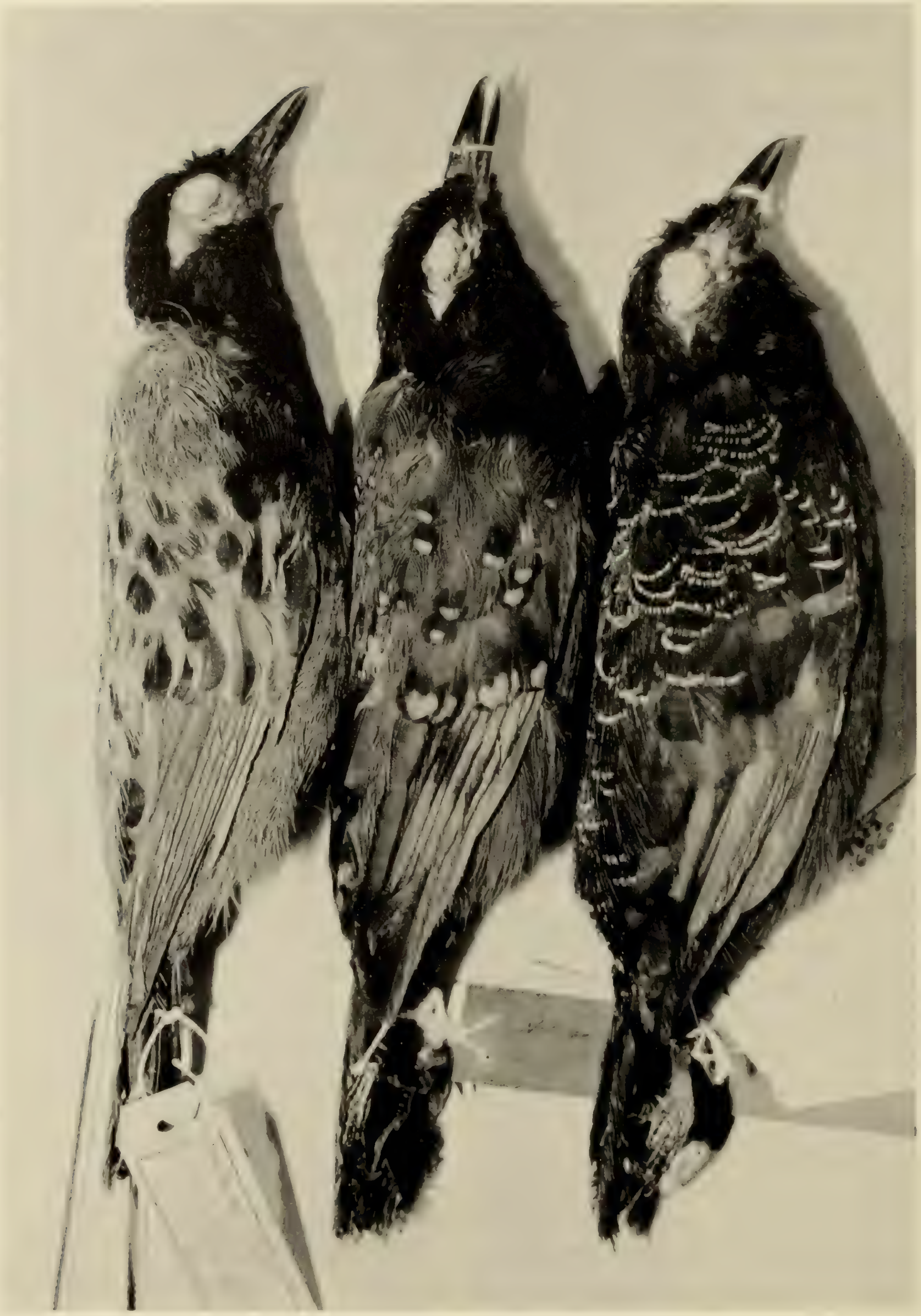

Fig. 1. Lateral views of adult males (from left to right): *Phlegopsis nigromaculata*, "*P. barringeri*" (ANSP 162,675; =*P. nigromaculata* × *P. erythroptera*), and *P. erythroptera*. Note ocelli on wing coverts and back of hybrid.

ocelli encircled by drop-shaped black spots on the feather tips of the mantle and wing coverts of the hybrid are not found in either parental species. By comparison, back feathers in *P. nigromaculata* are olivaceous-brown with a terminal black spot (rounded triangle). The color pattern in *P. erythroptera* is markedly different—back feathers are entirely black with a narrow white subterminal band (back feathers of juvenile males

Table 1.—Ranges and means of measurements (mm) of adult male *Phlegopsis nigromaculata, P. erythroptera,* and their hybrid (="*P. barringeri*"). *Phlegopsis* specimens are from Ecuador and north of the Río Amazonas in Peru. Significant *P*-values indicate that means of *Phlegopsis* species are different (two-tailed *t*-test).

	P-value	*Phlegopsis nigromaculata* ($n = 15$)	*Phlegopsis erythroptera* ($n = 8$)	*P. nigromaculata* × *P. erythroptera* (ANSP 162,675)
Wing	NS	87.1–94.0	88.6–93.6	
		90.9	91.4	93.7
Tail	<0.001	58.5–64.5	59.6–68.0	
		61.6	65.2	61.9
Tarsus	<0.001	29.2–32.4	30.1–33.3	
		30.6	32.2	31.2
Hallux	<0.01	18.5–20.9	19.7–21.3	
		19.8	20.6	20.4
Bill length	<0.05	12.0–14.6	11.9–13.7	
		13.2	12.6	12.8
Bill width	<0.01	4.6–5.7	4.5–5.0	
		5.2	4.8	5.2

have broad rufous edges, e.g., LSUMNS 110,210). Pattern elements in the hybrid may be interpreted by identifying probable homologues in the parental species. For example, the black spots of the hybrid and *P. nigromaculata* are probably homologous, while the buffy ocelli of the hybrid are homologous with the subterminal white bands in *P. erythroptera.* This suggests that during feather development in the hybrid, the subterminal band inherited from *P. erythroptera* invaginated to form an ocellus within the black spot. Less complete ocellations are found on the tertials and secondaries of the hybrid, where the terminal black spot failed to enclose the irregularly shaped ocellus.

This example offers rare insight into the complexity of genetic control of plumage patterns in antbirds. Because different pigments are believed to be encoded by different genes, even within the same feather tract (Buckley 1982), a minimum of five genes or gene complexes and their modifers appear to control the color pattern of back feathers in *Phlegopsis,* including those for: (1) ground color (expressed in both parental species and hybrid); (2) presence or absence of terminal spot (expressed in *P. nigromaculata* and hybrid); (3) color of terminal spot (expressed in *P. nigromaculata* and hybrid); (4) presence or absence of subterminal band or ocellus (expressed in *P. erythroptera* and hybrid); and (5) color of subterminal band or ocellus (expressed in *P. erythroptera* and hybrid). Serial patterns among feather tracts suggest that some genes affect several plumage tracts, for example, the terminal (or subterminal) black spots on the back, wings, and tail of *Phlegopsis nigromaculata.*

External morphology.—Variation of morphological characters of avian hybrids falls within the ranges exhibited by their parental species (Buckley 1982, Graves 1990), reflecting a polygenic mode of inheritance. As expected, the size of the hybrid antbird conformed to this pattern (Table 1). *Phlegopsis nigromaculata* and *P. erythroptera* are morphologically similar and the percent difference between their character means is small: wing (0.6%); tail (5.8%); tarsus (5.2%); hallux (4.0%); bill length (4.8%); and bill width (8.3%). Measurements of the hybrid fall at or between the means for five of the six characters measured on parental species. Meyer de Schauensee's (1951:3) observation that the hybrid had larger feet than other *Phlegopsis* is erroneous.

Most potential parental species are considerably smaller in all morphological di-

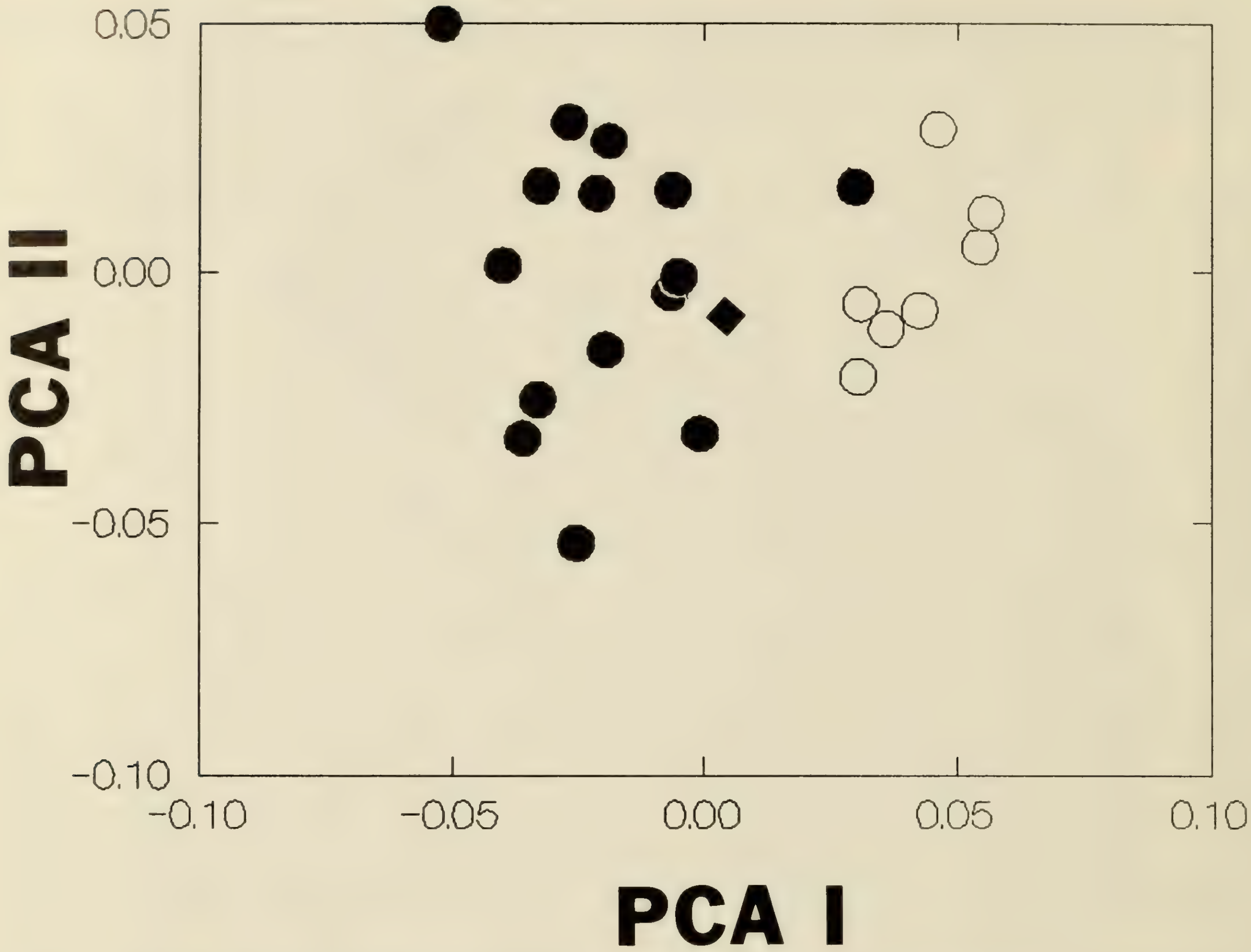

Fig. 2. Bivariate plot of principal component factor scores of *Phlegopsis nigromaculata* (=filled circles), *P. erythroptera* (=hollow circles), and their hybrid (=◇), "*P. barringeri.*"

mensions than the hybrid, including all taxa of *Myrmoborus, Hypocnemis, Myrmochanes, Sclateria, Percnostola, Pithys, Gymnopithys,* and *Rhegmatorhina. Myrmeciza fortis, M. melanoceps, M. hyperythra,* and *Myrmornis torquata* approach the size of *Phlegopsis,* but can be eliminated as parents of the hybrid on the basis of plumage characters. Morphological relationships of *Phlegopsis* species and the hybrid are shown by first two axes of a principal components analysis (Fig. 2, Table 2). Factor scores for the hybrid are nearly centered between the clusters of scores for the parental species. Intermediacy in complex shape variables, controlled by a multitude of genetic loci, constitutes strong evidence for the hybridization hypothesis. Had the factor scores of the hybrid fallen outside the envelope of scores of the proposed parental species, this particular hybrid hypothesis could have been rejected. From a statistical standpoint, the likelihood that a third valid species of *Phlegopsis* would be intermediate in size and shape between two other remarkably similar, sympatric species seems remote.

In summary, both plumage and morphological data are consistent with the hypothesis that *Phlegopsis barringeri* Meyer de Schauensee represents a hybrid between *Phlegopsis nigromaculata* and *P. erythroptera.* The name *Phlegopsis barringeri* is thus available only for the purpose of homonymy in taxonomy.

Discussion

Rarity of hybridization among the suboscines appears to be a real phenomenon rather than an artifact of taxonomic practices.

Table 2.—Factor loadings for the first two principal components from analysis of *Phlegopsis nigromaculata, P. erythroptera,* and their hybrid, "*P. barringeri*" (ANSP 162,675) (see Fig. 2).

Variable	Principal component axes I	Principal component axes II
Wing	0.001	0.006
Tail	0.013	0.006
Tarsus	0.012	0.008
Hallux	0.011	0.001
Bill length	−0.010	0.021
Bill width	−0.024	−0.001
Variance explained		
Percent	48.1	25.2

This position is supported not only by the cumulative record of avian hybridization (Gray 1958), but by several monographic works where extensive museum series of suboscine specimens were carefully studied (e.g., Wetmore 1972).

The causes of this phylogenetic correlation are unknown. However, I speculate that the absence of vocal learning among suboscines (Nottebohm 1972, Kroodsma 1988) may be a factor. These species develop basic patterns of vocalizations without auditory feedback and do not imitate songs or phrases of other species. Furthermore, geographic variation in song is reduced or absent (e.g., Lanyon 1978, Payne & Budde 1979), resulting in stereotypy of vocalizations within regional populations of a species. As a consequence, females may be less likely to make species recognition errors during mate selection. The prevalence of dull, weakly patterned, or sexually monomorphic plumages among the suboscines, especially the Thamnophilida and Furnariida, suggests that vocalizations are the primary isolating mechanism between species in this assemblage.

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SYSTEMATICS AND BIOGEOGRAPHY OF THE NEW ENGLAND COTTONTAIL, *SYLVILAGUS TRANSITIONALIS* (BANGS, 1895), WITH THE DESCRIPTION OF A NEW SPECIES FROM THE APPALACHIAN MOUNTAINS

Joseph A. Chapman, Kenneth L. Cramer, Nico J. Dippenaar, and
Terence J. Robinson

Abstract.—Multivariate statistical analyses of 19 cranial and toothrow measurements of 274 adult cottontails, hitherto referred to as *Sylvilagus transitionalis,* were undertaken. Our results provide clear evidence of two morphometrically distinct taxa within what has conventionally been regarded as a single species, *S. transitionalis,* and thus support previous investigations which had revealed two discrete karyotypes (2N = 46; 2N = 52). We consider the congruence in data sets to support the recognition of two sibling species in *S. transitionalis.* As here defined, the New England cottontail, *S. transitionalis* (2N = 52), is restricted to boreal habitat in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island and New York as far west as the Hudson River. The new Appalachian cottontail species, *Sylvilagus obscurus,* is generally an inhabitant of higher elevations and is restricted to the Appalachian Mountains and their associated mountain balds from the Hudson River through New York, Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama. The two species are phenotypically very similar but subtle differences in cranial shape, particularly in the anterior and medial portions of the skull, allow for their delineation. Diagnostic cranial ratios, indicated by multivariate procedures, in conjunction with the results from discriminant function analysis, provide a reliable and practical means of species identification in the absence of chromosomal data. In addition we speculate on the possible biogeographic processes in the New York area that may have contributed to the evolutionary divergence of these taxa during the Wisconsinan glaciation.

As currently understood, the New England cottontail, *Sylvilagus transitionalis,* is primarily an inhabitant of dense woodland and boreal environments (Chapman & Paradiso 1972, Chapman 1975, Chapman et al. 1982, Chapman & Ceballos 1990). The species is reported to range from southeastern New England south, along the Appalachians, to Alabama (Hall 1981, Chapman & Stauffer 1981). Within this region it has a mosaic distribution that is thought to reflect, in part, gradual climatic change since the last glaciation and the concomitant reinvasion of lowland areas by the more ubiquitous eastern cottontail, *S. floridanus.* These factors prompted Chapman & Stauffer (1981) to propose that *S. transitionalis* exists only as a refugial relict within the southern parts of its range.

More recently, however, the taxonomic status of *S. transitionalis* has been questioned by the finding of two distinct chromosomal races within its presumed geographic range; a northern race characterized by 2N = 52 (Holden & Eabry 1970, Wilson 1981, Ruedas et al. 1989) and a southern karyotype with 2N = 46 (Robinson et al. 1983, Ruedas et al. 1989). Based on this evidence Ruedas et al. (1989) concluded that the two chromosomal races occur parapatrically such that the northern karyotype extends roughly from the Wisconsinan terminal moraine northwards and the southern race from the same point southwards (Ruedas et al. 1989). Since there is no evidence of hybridization between the two karyotypes (Ruedas et al. 1989), it is probable that the chromosomal races represent two sibling species in what has traditionally been regarded as *S. transitionalis.*

The presence of two genetically distinct sibling species in *S. transitionalis* would profoundly affect the interpretation of many previous studies, especially those directed towards the conservation of a species which is considered vulnerable by virtue of its restricted distribution (Chapman & Stauffer 1981, Feldhamer et al. 1984, Webster et al. 1985, Mount 1986, Chapman & Ceballos 1990). Therefore, the aims of this study were: (1) to determine whether other parameters would similarly reflect evidence of a discontinuity following intraspecific analysis and, in so doing, further delineate the geographic distributions of the two reported karyotypes, (2) to attempt to identify the possible underlying factors that may have led to the present biogeography of these two species. A morphometric appraisal of a suite of cranial and dental measurements was undertaken on museum specimens whose collection localities span the entire range of what has been conventionally regarded as *S. transitionalis* and which includes the probable zone of parapatry suggested by the cytogenetic data (Holden & Eabry 1970, Robinson et al. 1983, Ruedas et al. 1989).

Methods

Where possible, 28 skull and toothrow measurements (Robinson & Dippenaar 1987) were recorded from each specimen from a preliminary data set (n = 283). All measurements were taken with dial calipers to the nearest 0.1 mm. Multivariate statistical analyses were performed using selected sub-routines of BIOΣTAT II (Pimentel & Smith 1986) and the Numerical Taxonomy System (NTSYS-pc; Rohlf 1986). The statistical procedures used in this investigation have been reported elsewhere (Robinson & Dippenaar 1983) and are similar to those used by Genoways (1973), Swanepoel & Schlitter (1978) and Dippenaar & Rautenbach (1986).

Those measurements found to have low repeatability (zygomatic arch length, posterior cranial height, interauditory breadth) were excluded from analysis. Furthermore, in order to remove excessive redundancy due to high correlations between measurements, a correlation matrix was calculated for all pairs of measurements derived from a subset of 30 specimens drawn from geographically contiguous populations in Wyndham and Tolland Counties, Connecticut, and clustered by the unweighted pair group method using arithmetic averages (UPGMA). Four length measurements (total length of skull, basal cranial length, maximum mandibular length, mandibular toothrow length) were highly correlated ($r \geq 0.84$); total length of skull was consequently retained as representative of these length measurements. Likewise, the relatively high correlations ($r \geq 0.71$) between palate vacuity length: palate incisor length; maxillary premolar length: maxillary premolar-molar length; palatal breadth: bizygomatic breadth, together with the numbers of specimens characterized by missing values for several of these measurements, led to further character exclusion and the retention of the second measurement in each case. As a result, a suite of 19 cranial and toothrow measurements from 274 adult specimens was finally retained for comprehensive analysis. These measurements included, total length of skull, muzzle length,

Table 1.—Delimitation of geographic populations (OTUs) for analysis in a 19-character Principal Component Analysis. OTUs represent grouped localities where these are geographically contiguous or, in instances involving more isolated populations, single localities even where these are represented by single specimens. The numbers representing each OTU's constituent populations correspond to those contained in the Gazetteer.

OTU no.	Constituent population(s)	OTU no.	Constituent population(s)	OTU no.	Constituent population(s)
1	1–2	15	73–74, 86	29	117
2	3–4	16	75–77, 79–80	30	118–119
3	91, 23–24	17	78, 81–84	31	116
4	5–6	18	87	32	120–121
5	7–8	19	88–89	33	122
6	25–26	20	90	34	123
7	9–12	21	92	35	124
8	13–18	22	93	36	126–127
9	19–22	23	94	37	125
10	27	24	95	38	128
11	28–29	25	96	39	131–132
12	30–32	26	115	40	129–130
13	34–43	27	97–109		
14	33, 44–72, 85	28	110–114		

frontal length, parietal length, posterior muzzle breadth, anterior frontal breadth, posterior frontal breadth, palate vacuity length, hard palate length, mesopterygoid space, maxillary premolar-molar length, principal I^1 breadth, palatal breadth, maximum cranial breadth, bulla breadth, maximum mandibular height, mandibular body breadth, I_1 breadth and mandibular premolar-molar length (see Robinson & Dippenaar 1987, for definition of measurements).

To reduce the effects of age variation, statistical analyses were conducted only on measurement of adults. Age was determined by using the fusion of the suture between the exoccipital and supraoccipital bones (Hoffmeister & Zimmerman 1967). Specimens of adults sorted by state of collection, were subsequently tested for secondary sexual dimorphism using a single classification analysis of variance. Only muzzle length and mesopterygoid space showed significant differences between the sexes ($P < 0.05$) thereby confirming other studies that span several lagomorph genera, all of which indicate that almost all disparities in measurement between the sexes are slight and statistically non-significant (Chapman 1971; Chapman & Morgan 1973; Taylor et al. 1977; Baker et al. 1978; Yates et al. 1979; Diersing & Wilson 1980; Robinson & Dippenaar 1983, 1987). The sexes were subsequently pooled and the combined data set subjected to further analysis.

Following preliminary analyses to ensure the homogeneity of individual and pooled samples, multivariate statistical analyses were performed, where possible, on arithmetic mean values for each measurement obtained from grouped localities (geographically contiguous samples). However, geographically isolated populations were treated independently, even when represented by single specimens. Using this approach, forty geographic populations (OTUs) were identified (Table 1) and analyzed by cluster and principal component analysis (PCA). Phenograms were generated from both the Pearson's product-moment correlation and average taxonomic distance matrices, and cophenetic correlation coefficients were calculated in order to assess the goodness of fit between phenograms (and PCA scattergrams) and the original standardized matrices. The PCA was based on correlation coefficients among characters. Two-dimensional projections of the samples on the first three components were made, and the correlation between the characters and these components as well as the percentage variation accounted for by them were computed. These analyses formed the basis of our taxonomic conclusions.

A discriminant function analysis was employed to assess the integrity of a priori designated groups. This was done by contrasting specimens derived from localities along the Appalachian mountains (high elevation areas; Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama—referred to as "Appalachian" = *Sylvilagus* sp. nov.) with those from predominantly low elevation regions (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, and New York—referred to as "non-Appalachian" = *S. transitionalis*). This grouping, loosely suggested by the cytogenetic data (Robinson et al. 1983, Ruedas et al. 1989), was supported by the PCA (Fig. 1). Furthermore, since the discriminant function analysis requires a full data set for each specimen classified, OTUs with missing values were excluded from the analysis resulting in a sample size of 216, of which 138 were a priori classified as "non-Appalachian" and 78 as "Appalachian."

To assist with species identification, diagnostic ratios between selected measurements were calculated. Likewise, the standardized canonical vectors generated by the discriminant function analysis are presented as an aid in species identification. While cytogenetic data provide for the unequivocal identification of "Appalachian" (*Sylvilagus* sp. nov.) or "non-Appalachian" (*S. transitionalis*) specimens, these are not always available, making the correct classification, particularly of museum specimens, problematic. However, by recording the 19 cranial and dental measurements on which the present analysis is based, animals lacking cytogenetic data, or museum specimens of dubious provenance, can be correctly classified with a high degree of accuracy. This can be done by: (1) subtracting the total sample mean of each measurement from the corresponding measurement of the unknown, (2) multiplying these derived values by the corresponding canonical vectors, (3) summing them for all 19 measurements and subsequently determining the group with which the unknown has the greatest affinity (Robinson & Dippenaar 1983).

Systematics

Both distance and correlation phenograms were computed from matrices based on standardized values. Although little structure was evident in the distance phenogram, clear separation of the OTUs originating from the Appalachian Mountains (*Sylvilagus* sp. nov.; OTU 21–40) from those in the "non-Appalachians" (*S. transitionalis*; OTU 1–20) was evident in the correlation phenogram (Fig. 2; cophenetic correlation coefficient 0.679). Cluster A comprised all those specimens initially defined as having been derived from "Appalachian" localities but excludes OTU 24 (Centre Co., Pennsylvania), which is represented by a single specimen (PM 3342) incorrectly clustered within the "non-Appalachian" assemblage B. Other misplaced OTUs, all "non-Appalachian" in designation, are OTU 4 (Sullivan Co., New Hampshire, USNM 508323 and 507723), OTU 19 (Westchester Co., New York, AM 5728 and Westchester Co., New York, USNM 188140 and 189138) and OTU 20 (Sullivan Co., New York, AM 69379). The two major clusters A and B are well differentiated from each other, joining at an average correlation of −0.15.

The amount of phenetic variation represented by the first two principal components was 50.6% (cophenetic correlation 0.856) while the third component contributed an additional 10.7% accounting, accumulatively, for 61.3% of the total phe-

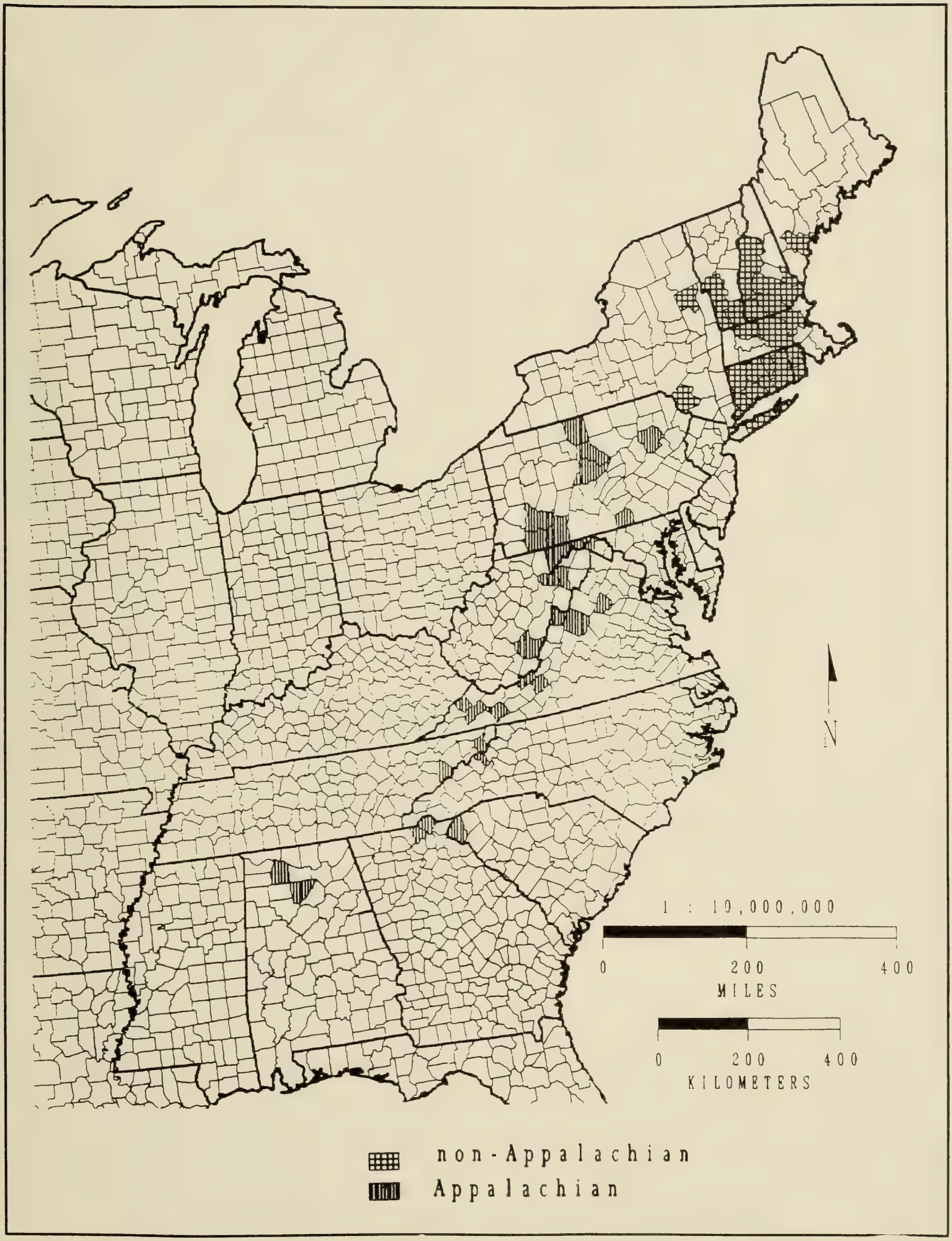

Fig. 1. Counties from which 274 specimens used in PCA and discriminant function analysis were collected, showing "non-Appalachian" and "Appalachian" a priori classification.

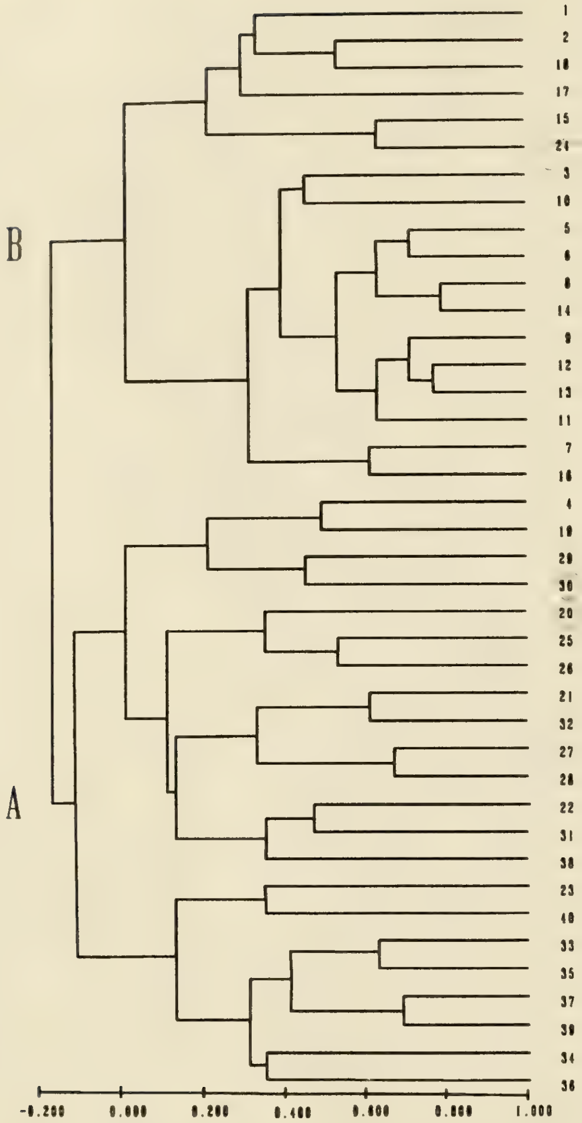

Fig. 2. Correlation phenogram with OTUs clustered by the unweighted pair-group method using arithmetic averages. OTUs 1–20 = *S. transitionalis*; OTU 21–40 = *S. obscurus*. See Table 1 for each OTU's constituent population(s).

Table 2.—Factor matrix from a 19-character principal component analysis based on values for each of 40 localities throughout the geographic ranges of *S. transitionalis* and *S. obscurus*.

Measurement	Factor I	Factor II
Total length of skull	0.894	−0.152
Muzzle length	0.632	−0.028
Frontal length	0.334	0.027
Parietal length	0.019	0.555
Post. muzzle breadth	0.622	−0.419
Ant. frontal breadth	0.162	0.147
Post. frontal breadth	−0.240	−0.563
Palate vacuity length	0.505	0.550
Hard palate length	0.460	−0.432
Mesopterygoid space	0.727	0.046
Max. premolar-molar length	0.873	0.158
Principal I^1 breadth	0.450	−0.583
Palatal breadth	0.788	0.272
Max. cranial breadth	0.714	0.138
Bulla breadth	0.628	−0.115
Max. mandibular height	0.550	−0.683
Mandibular body breadth	0.647	0.431
I_1 breadth	0.616	0.020
Mand. premolar–molar length	0.887	0.103

netic variation (Table 2, Fig. 3). The first component is largely influenced by size as indicated by the high positive loadings for most measurements, including total length of the skull, maxillary premolar-molar length and mandibular premolar length. The second component is more complex, highlighting shape differences principally in the anterior mid-portion of the skull. This is reflected in the relatively high positive loadings for parietal length, palate vacuity length and mandibular body breadth, and high negative values for posterior frontal breadth, posterior muzzle breadth, hard palate length, upper principal incisor breadth and mandibular height.

Examination of principal component plots (I:II; I:III; II:III) revealed that while there is little meaningful separation of OTUs along either component I or III, discrimination reflecting subtle shape differences between OTUs is evident on the second axis. With respect to the ordination along the second component (Fig. 3) a pattern similar to that shown in the correlation phenogram was found. Specifically, the "non-Appalachian" OTUs 1–20 are, almost exclusively, clustered in the bottom half of the two dimensional space and well separated from those derived from geographic populations designated as "Appalachian" (OTUs 21–40) which, with the exception of OTUs 26 and 29 (each represented by single specimens) are more loosely grouped in the upper half of the second component scale.

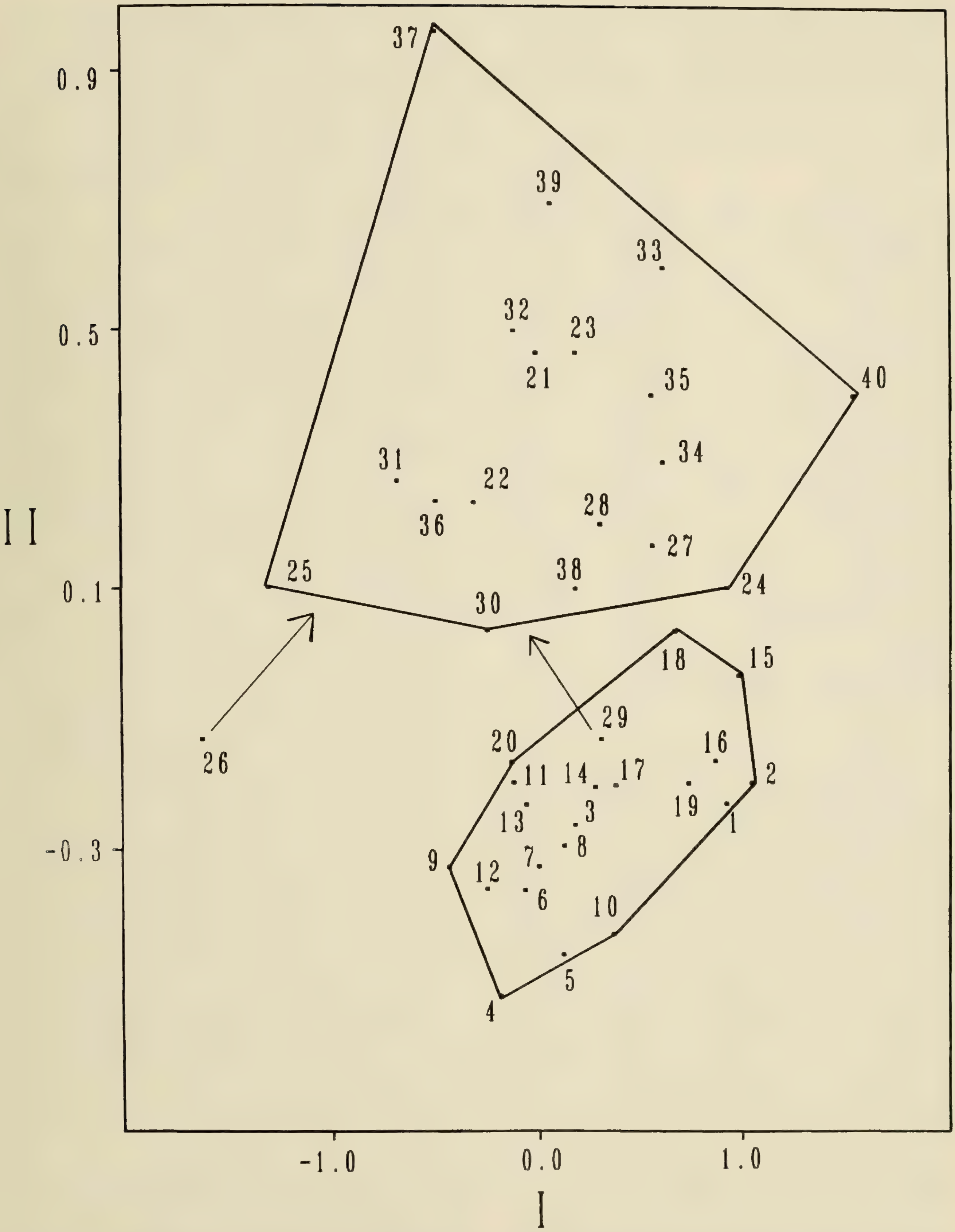

Fig. 3. Scattergram of components I and II from a principal component analysis based largely on sample means; OTUs 1–20 = *S. transitionalis*; OTU 21–40 = *S. obscurus*. See Table 1 for each OTU's constituent population(s).

Table 3.—Standardized canonical vectors for the 19 cranial and toothrow measurements resulting from a two-group discriminant function analysis of a priori grouped specimens of *S. obscurus* and *S. transitionalis* OTUs.

Measurement	Total sample means (mm)	Standardized canonical vectors
Total length of skull	70.964	−0.045
Muzzle length	25.991	0.157
Frontal length	33.244	−0.034
Parietal length	15.362	−0.114
Post. muzzle breadth	14.174	0.660
Ant. frontal breadth	15.307	−0.849
Post. frontal breadth	13.876	0.422
Palate vacuity length	17.406	−0.313
Hard palate length	6.040	1.026
Mesopterygoid space	6.866	0.390
Max. premolar-molar length	14.329	0.496
Principal I^1 breadth	2.695	4.785
Palatal breadth	20.519	−0.748
Max. cranial breadth	26.533	−0.482
Bulla breadth	8.393	0.074
Max. mandibular height	33.389	0.441
Mandibular body breadth	4.475	−0.511
I_1 breadth	2.593	−2.148
Mand. premolar–molar length	14.241	−0.264

Discriminant function analysis of 19 cranial and toothrow measurements from specimens characterized by full data sets was used to distinguish between the a priori groups of specimens categorized as "non-Appalachian" ($n = 138$) and "Appalachian" ($n = 78$). Standardized canonical vectors from this analysis are presented in Table 3. Of the 216 specimens used in the discriminant analysis, 210 (97.2%) were classified correctly and six (2.8%) incorrectly. The two groups were delineated by $DS_{0.5} = -0.50$ and with the exception of the OTUs listed below, the discriminant scores of the "non-Appalachian" group ranged from 3.78 to −0.34 (centroid = 1.29) whereas the scores of the "Appalachian" group ranged from −0.64 to −5.38 (centroid = −2.29). Of the six misclassified specimens, two "Appalachian" OTUs had discriminant scores only slightly larger than the DS_{05} value (0.26; 0.16), two "non-Appalachian" specimens had discriminant scores marginally below the $DS_{.05}$ value (−0.76 in both instances). More problematic was the aberrant classification of two "non-Appalachian" OTUs derived, respectively, from Cumberland Co., Maine (USNM 507686; discriminant score −1.71) and Sullivan Co., New York (AM 69379; discriminant score −1.48).

Two reasons, not necessarily mutually exclusive, may be advanced for the misclassification of the a priori grouped specimens. First, the anomalous classification may reflect possible measurement errors. Support for this hypothesis is that with one exception (Sullivan Co., AM 69379), the misclassified specimens formed part of a series, the constituents of which were derived from a single locality or, alternatively, contiguous localities in the same county. Second, the misclassification may reflect errors in our a priori assignment of specimens as "Appalachian" and "non-Appalachian" in the discriminant function analysis. There may be distributional overlap between the two forms such that the "Appalachian" karyotype (2N = 46) also exists as insular relicts in isolated montane habitat within the low-lying areas that accomodates the 2N = 52 form.

Our analyses support the identification of two phenetic entities within what conventionally has been referred to as *S. transitionalis*. We believe that specimens to the north and northeast of the Hudson River form a discrete species which, given the existing cytogenetic data, is characterized by a 2N = 52 karyotype (Holden & Eabry 1970, Wilson 1981, Ruedas et al. 1989). We refer these specimens to *S. transitionalis,* with the type locality being Liberty Hill, New London Co., Connecticut (Bangs 1895). This includes localities characterized by both relatively high montane habitat (Vermont and New Hampshire) and low-elevation terrain (Maine, Connecticut, Massachusetts, Rhode Island). Specimens derived from localities west and south of the Hudson River, at points along the reaches of the Appalachian mountain chain as far south as Georgia and

Table 4.—Skull measurements of *S. transitionalis* and *S. obscurus*. *SD* = standard deviation, *CV* = coefficient of variation and *n* = sample size.

Measurement	Mean (mm)	*SD*	*CV*	*n*	Range (mm)
A: *S. transitionalis*					
Total length of skull	70.95	1.99	2.81	174	75.90–65.80
Muzzle length	26.10	1.41	5.39	178	30.22–21.66
Frontal length	33.21	1.57	4.72	175	37.01–29.49
Parietal length	15.42	0.79	5.21	175	17.63–12.28
Post. muzzle breadth	14.32	0.74	5.16	178	16.46–12.63
Ant. frontal breadth	14.79	0.85	5.72	176	17.02–12.78
Post. frontal breadth	13.97	0.82	5.84	174	16.43–11.86
Palate vacuity length	17.27	0.77	4.46	178	19.18–15.40
Hard palate length	6.17	0.41	6.69	179	7.15–5.12
Mesopterygoid space	6.82	0.48	7.04	179	8.01–5.74
Max. premolar-molar length	14.32	0.60	4.16	179	16.02–12.90
Principal I^1 breadth	2.74	0.13	4.74	177	3.06–2.34
Palatal breadth	20.38	0.63	3.10	179	21.88–18.97
Max. cranial breadth	26.47	0.66	2.51	165	29.02–24.84
Bulla breadth	8.35	0.26	3.13	167	9.31–7.68
Max. mandibular height	33.63	1.13	3.36	168	36.26–30.66
Mandibular body breadth	4.46	0.21	4.77	173	5.04–3.84
I_1 breadth	2.59	0.13	4.97	172	2.92–2.20
Mand. premolar–molar length	14.22	0.54	3.82	171	15.64–12.84
B: *S. obscurus*:					
Total length of skull	70.82	2.05	2.89	91	75.16–65.50
Muzzle length	25.81	1.52	5.88	95	30.68–21.02
Frontal length	33.32	1.57	4.71	93	37.04–28.86
Parietal length	15.53	0.97	6.24	90	18.44–13.42
Post. muzzle breadth	13.95	0.88	6.30	95	15.92–11.89
Ant. frontal breadth	16.22	1.15	7.11	92	19.12–13.63
Post. frontal breadth	13.71	0.86	6.24	94	15.56–12.22
Palate vacuity length	17.65	0.78	4.41	93	19.58–15.76
Hard palate length	5.76	0.38	6.62	94	6.76–5.04
Mesopterygoid space	6.96	0.42	6.00	95	8.37–6.14
Max. premolar-molar length	14.33	0.56	3.94	95	15.95–13.11
Principal I^1 breadth	2.62	0.14	5.40	95	2.89–2.26
Palatal breadth	20.76	0.66	3.16	95	22.01–18.87
Max. cranial breadth	26.70	0.74	2.76	92	28.72–24.81
Bulla breadth	8.41	0.31	3.73	93	8.99–7.68
Max. mandibular height	32.95	1.20	3.63	92	35.79–30.09
Mandibular body breadth	4.50	0.21	4.63	95	5.21–4.06
I_1 breadth	2.61	0.11	4.36	95	2.94–2.38
Mand. premolar–molar length	14.26	0.51	3.59	94	15.87–13.23

Alabama are phenetically distinct from *S. transitionalis* and, although cytogenetic data from Pennsylvania, North Carolina and further south are not available, are all considered likely to possess the 2N = 46 karyotype (Robinson et al. 1983, Ruedas et al. 1989). We refer these high-elevation specimens to the Appalachian cottontail.

There is considerable overlap in the observed ranges of all 19 characters used in this study (Table 4) indicating the difficulties associated with discriminating between the two species without resorting to cytogenetic analyses. However, unlike the absolute values, proportionate differences of diagnostic value are evident when ratios are

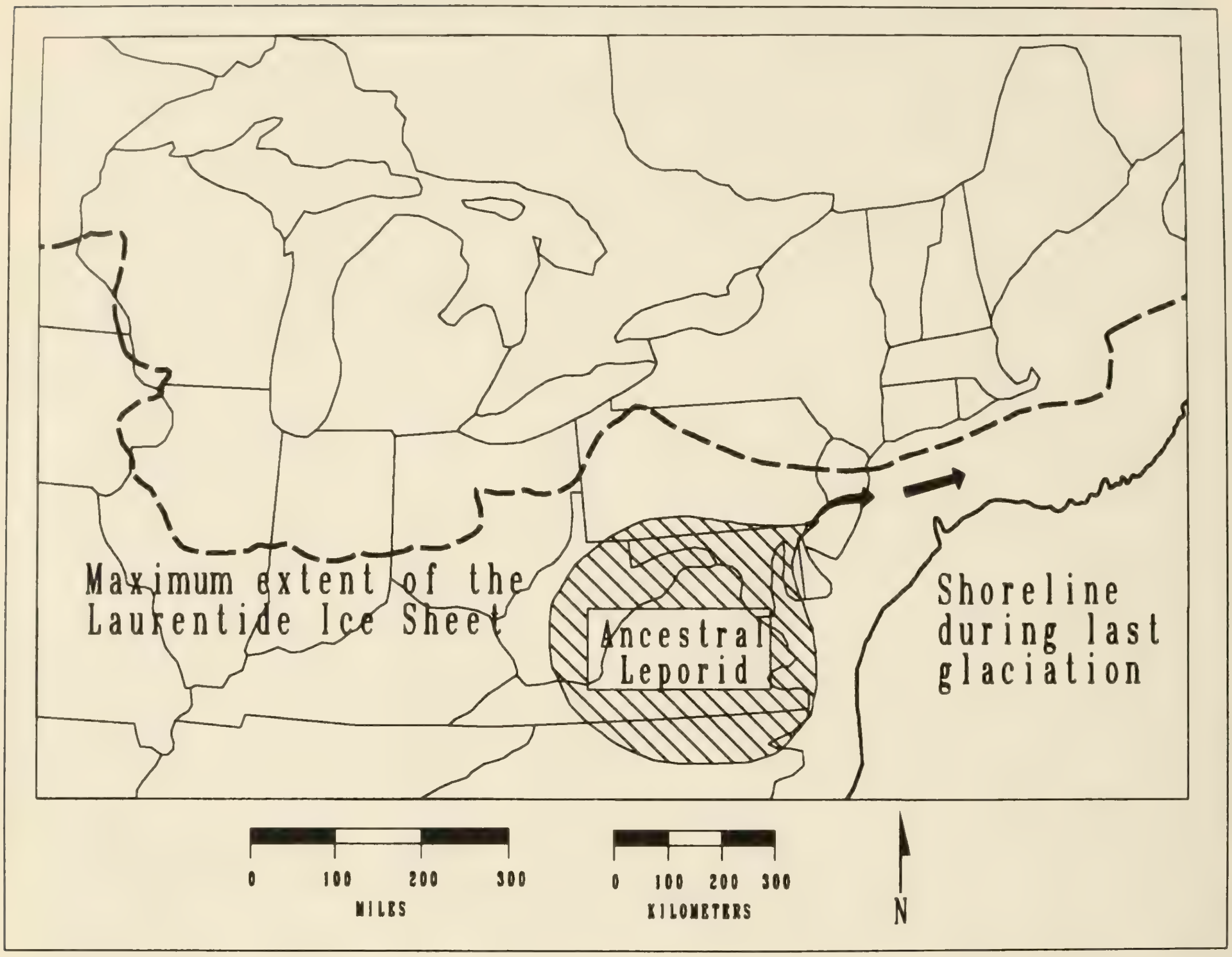
Maximum extent of the Laurentide Ice Sheet
Ancestral Leporid
Shoreline during last glaciation
0 100 200 300
MILES
0 100 200 300
KILOMETERS
N

Fig. 4. Hypothesized invasion of the ancestral *transitionalis/obscurus* leporid along the eastern edge (dotted line) of the Laurentide ice sheet. Map details from Knebel (1981) and Morgan (1987).

calculated by contrasting selected measurements with high positive loadings on component II against those with high negative loadings (Table 2). In the Appalachian cottontail the skull is proportionately shorter anteriorly, and medially narrower, than in *S. transitionalis.* Two of the ratios characterized by no overlap in mean ± one standard deviation (I^1 breadth: anterior frontal breadth, and hard palate length: anterior frontal breadth) are particularly useful in taxon delineation (Table 5).

Biogeography

Our proposal that the Hudson River delineates the geographic distributions of the two species does not imply that the waterway is now completely effective in restricting movement between karyotypes, although it undoubtedly has been in the evolutionary past (Teller 1987). In this regard, included in our analysis are several specimens from New York State localities marginally east and west of the Hudson River (Sing Sing and Hastings, Westchester Co. (east) represented by OTU 19 in the PCA; Monticello, Sullivan Co. (west) represented by OTU 20 in the PCA) considered by us to be low elevation "non-Appalachian" specimens (*S. transitionalis*) but which, interestingly, behave somewhat inconsistently in the two types of analysis used in this investigation. While hybridization between the species cannot be excluded, given the magnitude of the chromosomal differences that distinguish the respective genomes (Ruedas et al. 1989), it is unlikely.

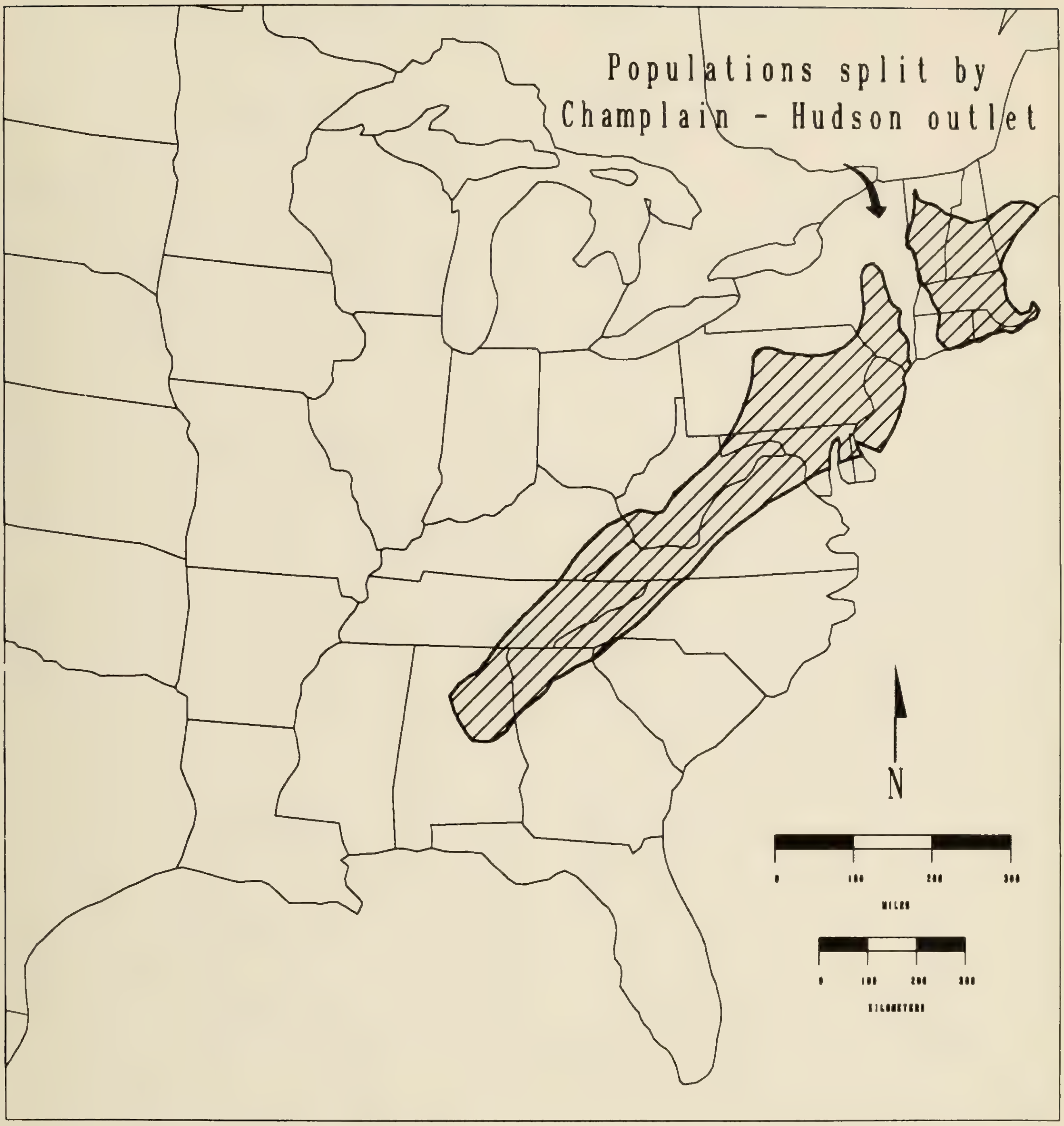

Fig. 5. Proposed geographic isolation of the ancestral *transitionalis/obscurus* populations by the eastward shift in the Champlain-Hudson outflow. Map details from Teller (1987) and Hall (1981).

Although simple fusion of heterozygotes often segregate in a balanced fashion, the paracentric inversion difference involving one of the fusion elements (chromosome 4 of Ruedas et al. 1989) is likely to result in more complex meiotic configurations and impaired fertility of the heterozygotes (Robinson et al. 1991). However, irrespective of these considerations, future studies directed at refining the contact zones between the species should involve extensive sampling along the borders of the Hudson River and Lake Champlain.

We believe that a series of events similar to those illustrated in Figs. 4–6, occurred over the last 18,000 to 10,000 yr and resulted in the evolution of these two sibling species. We hypothesize that the ancestral

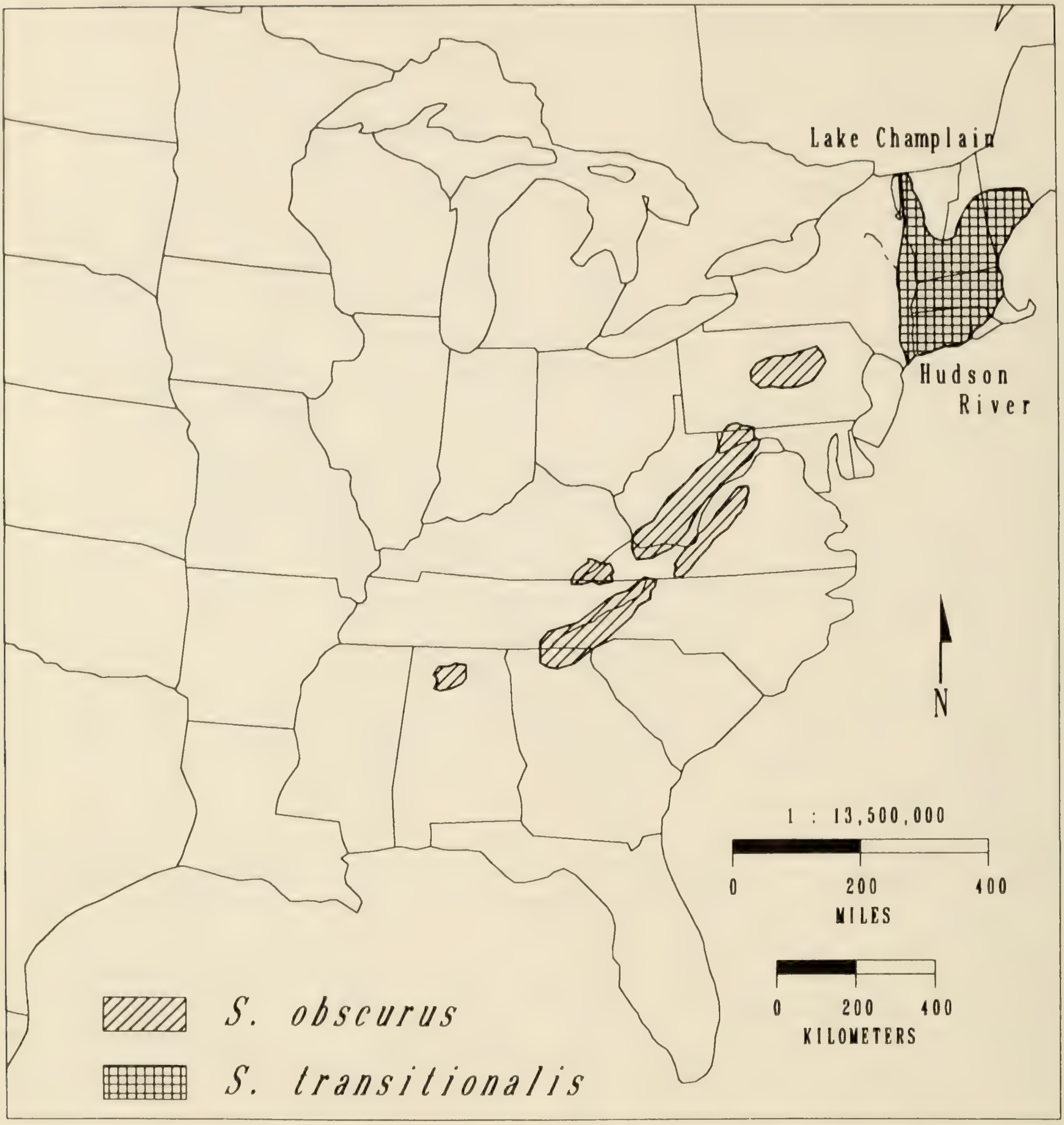

Fig. 6. Current distribution of *S. transitionalis* and *S. obscurus.* Distribution map based on this study and data collected by Chapman and Stauffer (1981).

leporid invaded northwards along the Laurentide ice sheet about 18,000 yr B.P. (Fig. 4; Morgan 1987). As the Laurentide ice sheet receded 10,000–12,000 yr B.P., and the outflow shifted eastward from the Champlain-Hudson Valley System (Fig. 5; Teller 1987), this split the ancestral leporid group into two populations which later led to the evolution of the extant *S. transitionalis* and the species described herein.

In essence, the conclusions drawn from our morphometric analysis concur with those of Ruedas et al. (1989). These authors propose that the two karyotypes occur parapatrically, with the northern karyotype (2N = 52) extending from the Wisconsinan terminal moraine northwards, and the southern karyotype (2N = 46) from the same point south. They suggest that the 2N = 52 karyotype (*S. transitionalis*) arose sometime in the late Wisconsinan and subsequently dispersed northwards with the development of oak-chestnut forests as the ice-shelf retreated. However, we propose that the splitting of the ancestral leporid by the Champlain-Hudson outflow is an equally likely hypothesis as to how these two species arose in allopatry. The 2N = 46 karyotype was, as in this study, similarly regarded by Ruedas et al. (1989) as being largely restricted to animals from high elevation Appalachian habitat.

The proposed contact zone between two species is illustrated in Fig. 7 together with collection localities from this region which are incorporated in the present study. The Hudson River flows through a deep glacial cut in the area from Albany, New York south to the Atlantic Ocean and is subject to tidal influence. The area in, and around, Warren and Essex Counties, New York, is not characterized by a major river valley and movement between *Sylvilagus* sp. nov. and *S. transitionalis* could undoubtedly occur. Thus, we hypothesize that overlap of the two species has occurred in this region and it is likely that the two groups have moved down along both banks of the Hudson River sometime in the last 5,000–10,000 yr and this may represent a natural contact zone between them. Handley (1971:285) points out that there are numerous examples of "closely related pairs of species in the Appalachians" and that "most of them show some degree of competitive exclusion."

Given our delineation of the two taxa (*S. transitionalis* north and northeast of the Hudson River; *Sylvilagus* sp. nov. strictly Appalachian in distribution), it is noteworthy that material referable to either species from the lower elevations and plains abutting the eastern reaches of the Appalachian mountains and eastward to the Eastern Seaboard, appears absent from current museum collections. While this may merely reflect a sampling bias, it is also possible that competition with the eastern cottontail, *S. floridanus,* may have hampered the expansion of both species into these areas and the two in fact, may be absent from this region (Handley 1971, Chapman & Morgan 1973, Chapman & Fuller 1975).

Habitat

The description of the habitat of *S. transitionalis* reported by Chapman & Stauffer (1981) included the geographic range of the new cottontail. Consequently, we attempt to more accurately define habitat preferences of both species. Several detailed habitat studies of *S. transitionalis* in New England (the range of *S. transitionalis* s. s.), have been published (Fay & Chandler 1955, Nugent 1968, Linkkila 1971, Johnston 1972, Jackson 1973). These authors found no clear relationship of *S. transitionalis* to any forest region or land use as was detailed by Johnston (1972) for the species in southern New England. Jackson (1973) reported declining New England cottontail populations and believed the decline resulted from habitat change associated with older forest types. He indicated that the species was commonly associated with pines (*Pinus* spp.), grasses, hardwoods (general), birches (*Betula* spp)., oaks (*Quercus* spp.), blackberry and raspberry (*Rubus* spp.), panicled dogwood (*Cornus racemosa*), alders (*Alnus* spp.), common juniper (*Juniperus comminis*), sugar maple (*Acer saccharum*), nursery plantings, cherries (*Prunus* spp.), goldenrod (*Solidago* spp.), sweetfern (*Comptonia peregina*), staghorn sumac (*Rhus typhina*), maple-leafed viburnum (*Viburnum acerifolium*), bracken fern (*Pteridium aouilinum*), asters (*Aster* spp.), high-bush blueberry (*Vaccinium corynmbosum*), hawthorn (*Crataegus* spp.), apple (*Pyrus malus*), and mosses (Jackson 1973, Table 3). Furthermore, the species has been recorded in virtually all habitat types in southern Connecticut (Nugent 1968).

In contrast, the Appalachian cottontail is strictly associated with dense cover and conifers at higher elevations along the Appalachian mountain chain (Llewellyn & Han-

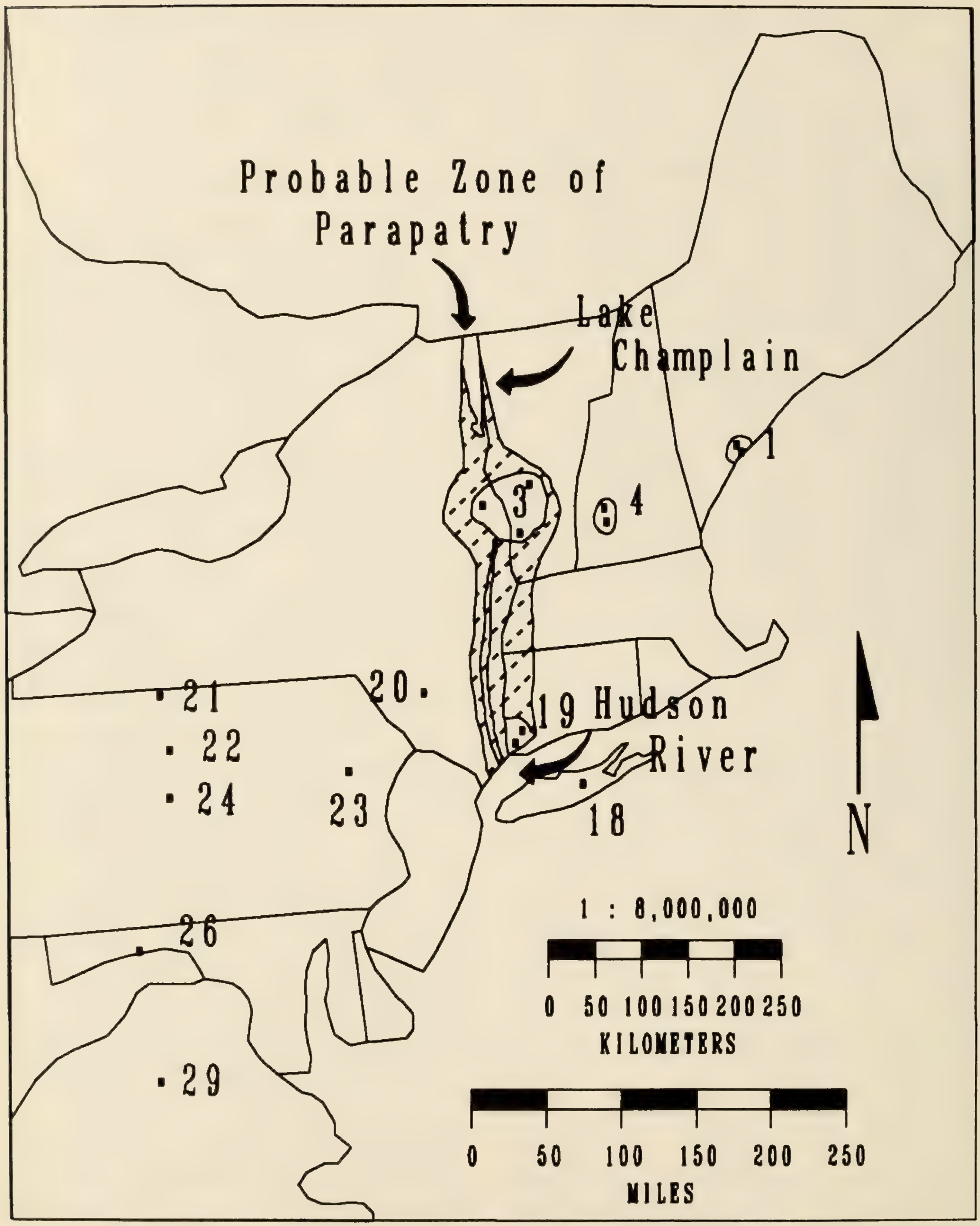

Fig. 7. Detailed map of the likely zone of parapatry between *S. transitionalis* and *S. obscurus*. See Table 1 and Gazetteer for populations comprising each geographic OTU.

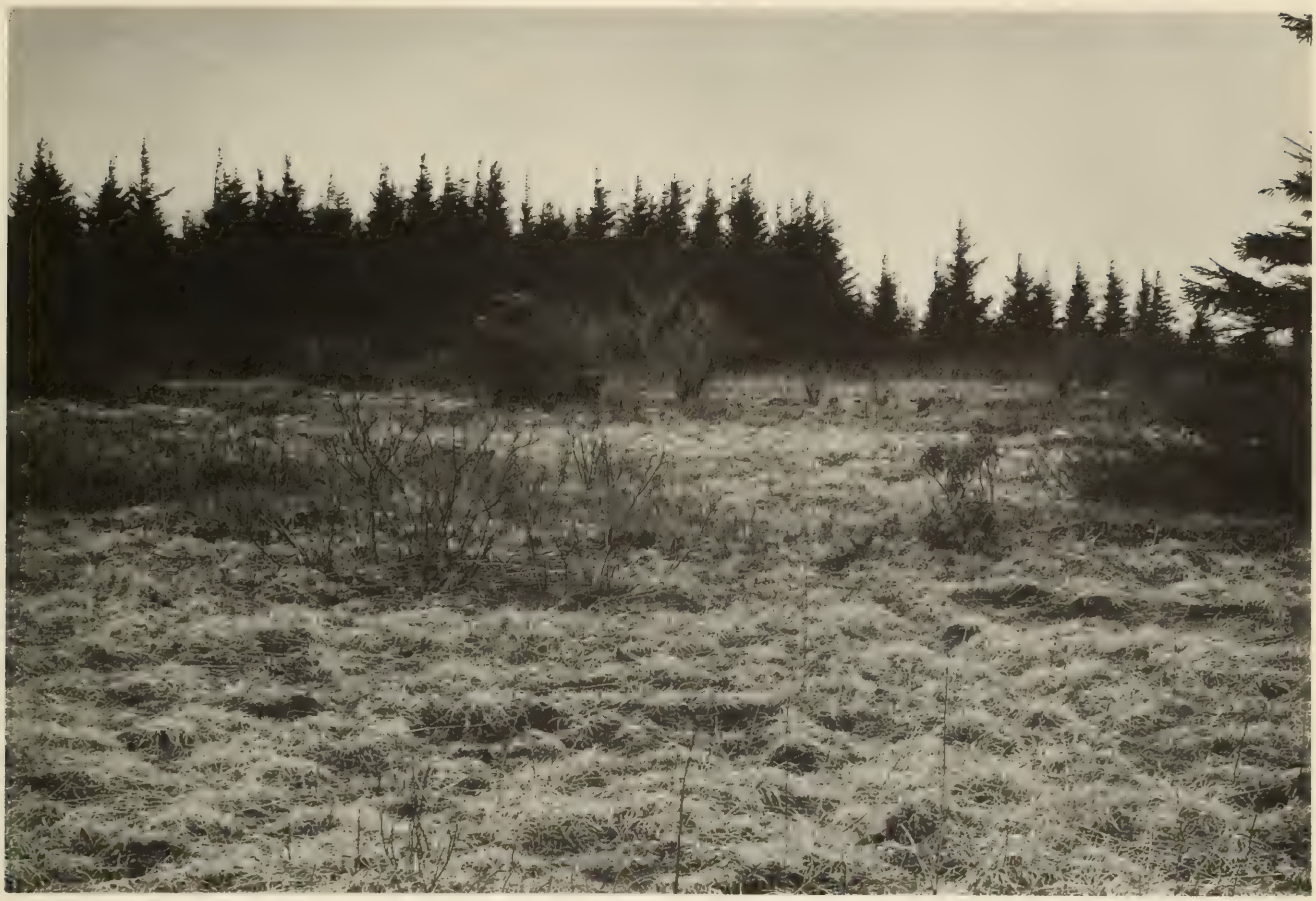

Fig. 8. Photograph of the type locality of the Appalachian cottontail, *S. obscurus,* at the Dolly Sods Scenic Area, Grant Co., West Virginia.

dley 1945, Chapman & Stauffer 1981, Fig. 8). In Maryland, West Virginia, Georgia and Alabama the species is associated with conifers and heath habitat, especially *Kalmia* and *Vaccinium,* both characteristic species of high elevation or boreal environments (Chapman & Morgan 1973, Chapman & Stauffer 1981). In Virginia, the Appalachian cottontail occurs within 6–7 year old clear-cuts in the higher elevations (Blymyer 1976). Howell (1921) reported the species on mountain slopes and associated foothills in Alabama. Chapman & Morgan (1973:11–12) described the habitat of the Appalachian cottontail type locality (Fig. 8) in detail as: "a high wind-swept plateau along the Allegheny Front in northern West Virginia. The exposed bedrock reaches to over 1100 m in elevation. The area abounds with small ponds and streams. Most of the vegetation has suffered mechanical damage from winterkill and the persistent, strong winds from the west. Originally, the area was completely covered with a climax forest of red spruce (*P. rubens*). The entire area was denuded of trees by heavy logging and subsequent fires in the late 1800's. The forest destruction resulted in the existence of large areas of heath and scrubby trees maintained by periodic fires. The heath plains and bogs host rhododendron, mountain laurel, blueberry *Vaccinium corymbosum,* arbutus *Epigaca repens,* winterberry *Ilex verticillata,* deerberry *V. stamineum,* and cranberry *V. oxycoccus.* Throughout the heath, red spruce, hemlock, and pines grow singly or in groups. Forested areas bordering the heath plains consisted mainly of yellow birch, beech, fire cherry (*P. pennsylvanica*), red maple, striped maple, serviceberry (*Amelanchier humilis*), mountain ash (*P. americana*), mountain holly (*I. montana*), aspens (*Populus* spp.) and hawthorn. The New England [=Appalachian] cottontail predominates on the plateau and is abundant in the heather and low scrub." From these accounts it is clearly apparent that the Appalachian species is associated with conifers and ericaceous vegetation characteristic of high altitude or boreal habitats.

Species Descriptions

Sylvilagus transitionalis (Bangs, 1895)
New England Cottontail

Lepus sylvaticus transitionalis, Bangs, 1895; 405.

Sylvilagus transitionalis, Nelson 1909:195.

Holotype.—MCZ B 2407 adult, male, skin and skull, from Liberty Hill, New London Co., Connecticut. Collected 6 Nov 1894 by O. Bangs. (See remarks.)

Topotypes.—MCZ B 1206 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 1207 adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2408, adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2409, adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2410 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2411 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5613 female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5635 adult, male, skull, Liberty Hill, New London Co., Connecticut. MCZ B 5635 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B5640 adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5641 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5642 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut.

Range.—Previously widely distributed in New England north to Rutland, Vermont, southern New Hampshire, extreme southwestern Maine, southwest through eastern New York (Nelson 1909) to the eastern bank of the Hudson River. Currently restricted to boreal habitat in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island and in New York as far west as the Hudson River (Fig. 9).

Diagnosis.—Medium-sized cottontail with dorsal parts pinkish buff to ochraceous buff, overlain with black hairs giving the species a lined effect. There is a distinct black edge on the ears and usually a distinct black spot between the ears. The postorbital process is thin and tapering and the supraorbital process is lacking or jagged or irregular in outline (Chapman 1975).

Remarks.—Bangs (1895:408) lists the type of *S. transitionalis* No. 2407 as an adult female; however, the skin and skull are both identified as a male. Topotype B2409 is an adult female not a male. B 11 was collected in 1893. B 1800 was exchanged to E.R. Warner in 1910. The distribution of *S. transitionalis* as herein described is much reduced from that previously reported (Nelson 1909, Chapman & Morgan 1973, Chapman 1975, Chapman & Stauffer 1981, Chapman et al. 1982, Chapman & Ceballos 1990). There has not been a population of *S. transitionalis* at the type locality for some time (Johnston 1972). O. Bangs designated the series of topotypes listed above which would appear to represent the paratypes for *S. transitionalis.*

Specimens examined.—Holotype, topotypes, and 173 specimens from localities listed below. The numbers following county names refer to numbers of specimens examined from each locality.

Maine: Cape Elizabeth, Cumberland Co., 2 (USNM); Gray, Cumberland Co., 1 (USNM).

New Hampshire: Enfield, Grafton Co., 1 (USNM); West Lebanon, Grafton Co., 1 (UM); Newport, Sullivan Co., 1 (USNM);

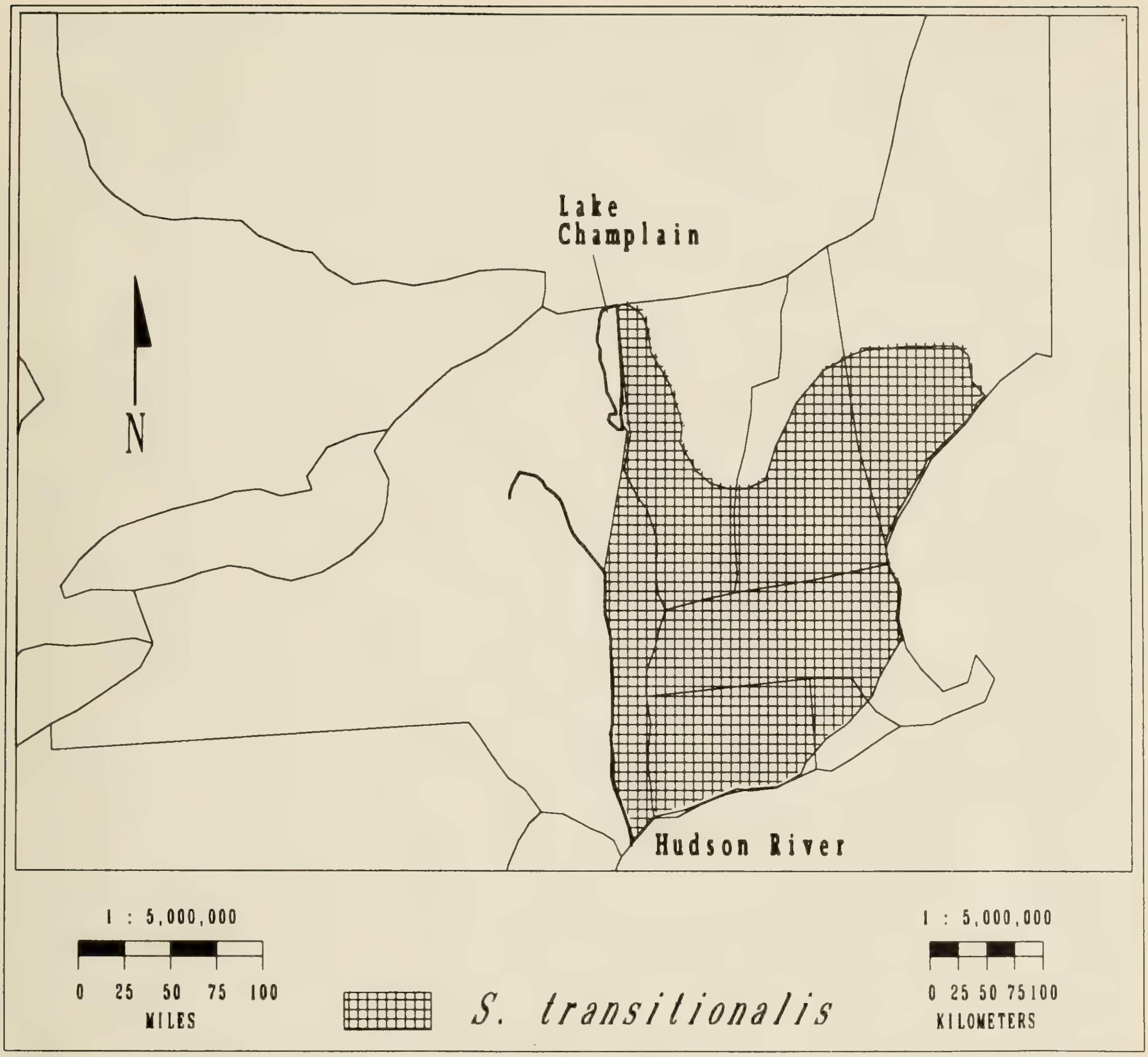

Fig. 9. Current distribution of *S. transitionalis.* Distribution map based on this study and data collected by Chapman and Stauffer (1981).

Lempster, Sullivan Co., 1 (USNM); Concord, Merrimack Co., 1 (USNM); Bow, Merrimack Co., 1 (USNM); Swanzey, Cheshire Co., 2 (USNM); Rindge, Cheshire Co., 1 (USNM); Walpole, Cheshire Co., 1 (USNM); Cold River, Cheshire Co., 1 (USNM); Nashua, Hillsborough Co., 2 (USNM); Hancock, Hillsborough Co., 1 (USNM); Manchester, Hillsborough Co., 1 (USNM); Greenville, Hillsborough Co., 1 (USNM); Litchfield, Hillsborough Co., 1 (USNM); Milford, Hillsborough Co., 1 (USNM); Somersworth, Strafford Co., 1 (USNM); Durham, Strafford Co., 1 (USNM); Windham, Rockingham Co., 1 (USNM); Greenland, Rockingham Co. 1 (UM).

Vermont: Dorset, Bennington Co., 1 (USNM); Mendon, Rutland Co., 1 (USNM); Vernon, Windham Co., 2 (USNM); Saxtons River, Windham Co., 1 (CFM).

Rhode Island: Charleston, Providence Co., 1 (USNM); Wallum Lake, Providence Co., 1 (USNM); Worden Pond, Washington Co., 1 (USNM); Exeter, Washington Co., 7 (USNM); Richmond, Washington Co., 5 (USNM); North Kingston, Washington Co., 6 (USNM); Wolf Rock, Washington Co., 1 (USNM); Arcadia, Washington Co., 1 (USNM); Middlebridge, Washington Co., 1

(USNM); Pettasquamsutt, Washington Co., 1 (USNM); Washington Co., 4 (USNM).

Massachusetts: Rowe, Franklin Co., 2 (USNM); Birch Hill, Worcester Co., 6 (USNM); Royalston, Worcester Co., 1 (USNM); Wilmington, Middlesex Co., 11 (USNM); Dunstable, Middlesex Co., 2 (USNM); Shirley, Middlesex Co., 1 (USNM).

Connecticut: Barn Island, New London Co., 7 (USNM); Waterford, New London Co., 2 (USNM); Pawcatuck, New London Co., 1 (PM); Niantic, New London Co., 2 (PM); Franklin, New London Co., 1 (USNM); Salem, New London Co., 1 (USNM); Norwich, New London Co., 1 (USNM); Plainfield, New London Co., 2 (USNM); Stonington, New London Co., 1 (USNM); Ashford, Windham Co., 2 (USNM); Pomfret-Abington, Windham Co., 1 (USNM); Sterling, Windham Co., 3 (USNM); Windham, Windham Co., 1 (USNM); Warrenville, Windham Co., 3 (USNM); Thomson, Windham Co., 3 (USNM); Woodstock, Windham Co., 1 (USNM); Westford, Windham Co., 4 (USNM); Lebanon, Windham Co., 1 (USNM); Chaplin, Windham Co., 1 (USNM); Killingly, Windham Co., 1 (USNM); Mansfield, Tolland Co., 2 (USNM), 1 (PM); Storrs, Tolland Co., 9 (USNM); Stafford Springs, Tolland Co., 4 (USNM); Amston-Hebron, Tolland Co., 1 (USNM); Horsebarn Hill, Storrs, Tolland Co., 2 (USNM); Willington, Tolland Co., 1 (USNM); Westbrook, Middlesex Co., 1 (AM); East Haddam, Middlesex Co., 1 (USNM); Killingsworth, Middlesex Co., 1 (USNM); North Granby, Hartford Co., 1 (USNM); New Haven, New Haven Co., 1 (PM); Southbury, New Haven Co., 2 (USNM); Milford, New Haven Co., 1 (PM); Sharon Mountain, Litchfield Co., 2 (AM); Macedonia Brook State Park, Litchfield Co., 1 (AM); Torrington, Litchfield Co., 2 (USNM); Cornwall, Litchfield Co., 1 (USNM); Canaan, Litchfield Co., 1 (USNM); Woodbury, Litchfield Co., 1 (USNM); Easton, Fairfield Co., 3 (USNM); Fairfield-Larsen WS, Fairfield Co., 3 (USNM); Fairfield, Fairfield Co., 3 (USNM); Danbury, Fairfield Co., 1 (USNM).

New York: Monticello, Sullivan Co., 1 (AM); Mastic, Suffolk Co., 3 (AM); Hastings, Westchester Co., 1 (AM); Sing-Sing, Westchester Co., 2 (USNM).

Sylvilagus obscurus, new species
Appalachian Cottontail
Fig. 10

Holotype.—USNM 567187, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia. Collected 8 Apr 1974 by Joseph A. Chapman. Field no. DS-58.

Allotype.—USNM 567189, male, skin and skull, from near Davis, Tucker Co., West Virginia. Collected 17 Aug 1974 by Joseph A. Chapman. Field No. DS-82.

Paratypes.—USNM 567195, adult, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-97. USNM 567186, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-46. USNM 567196, adult, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. CAZ 7. USNM 567185, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-45. USNM 567183, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-28. USNM 567198, adult, male, skull, Route 93 near Tucker Co. line, Grant Co., West Virginia, Field no. DS-69. USNM 567184, adult, male, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-33. USNM 567197, adult, male, skull, from near Davis, Tucker Co., West Virginia, Field no. CAZ 11. USNM 567191, female, skin and skull, near Davis, Tucker Co., West Virginia, Field no. DS-86. USNM 567192, immature, female, skin and skull, near Davis, Tucker Co., West Virginia, Field no. DS-

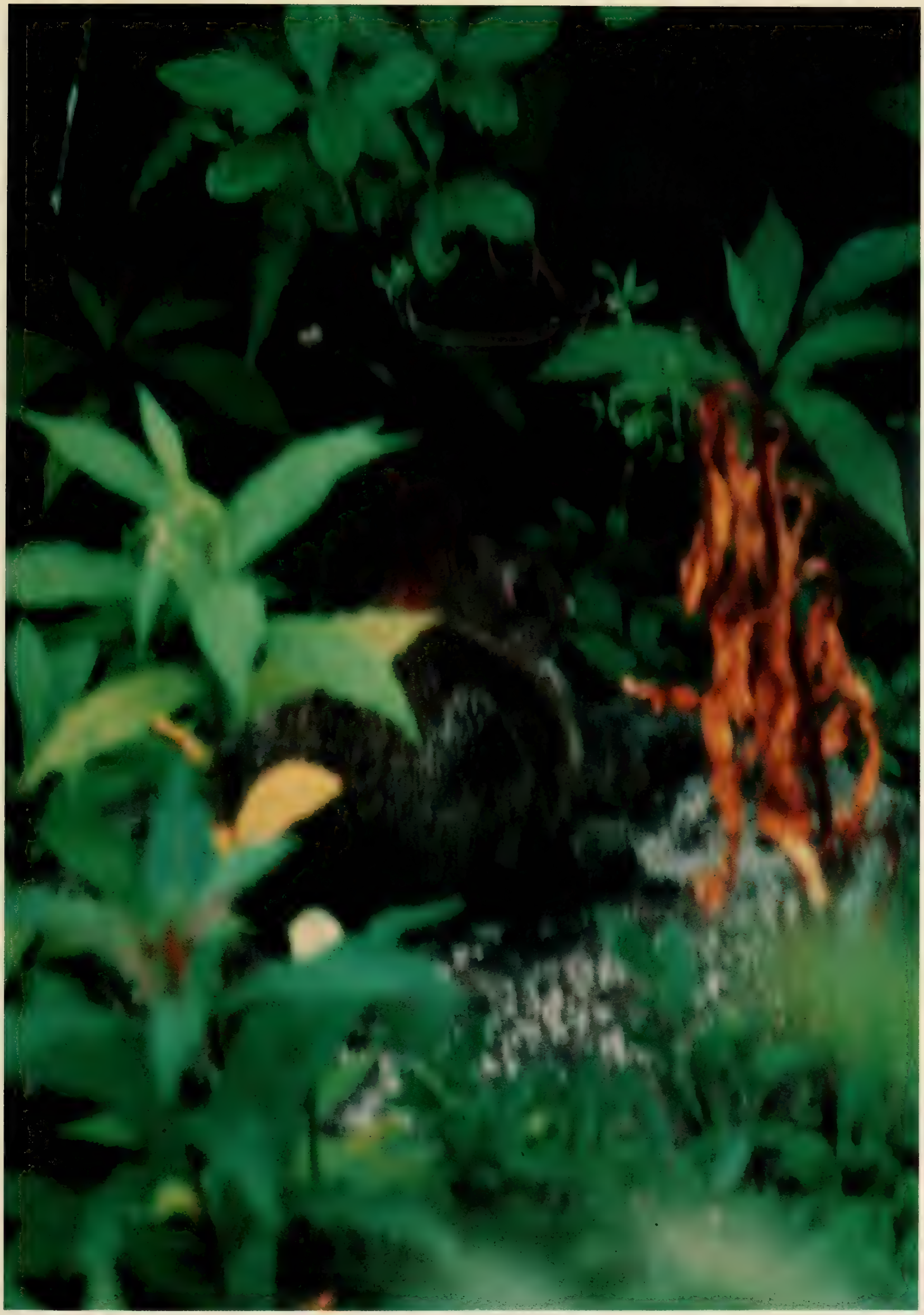

Fig. 10. Photograph of the Appalachian cottontail, *Sylvilagus obscurus,* taken at Spruce Knob, West Virginia, near the type locality (elevation 1463 m). Photograph by Joseph A. Chapman.

88. USNM 567194, immature, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-94. USNM 567190, immature, female, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-83. USNM 567188, immature, female, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-77. USNM 567193, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-93.

Range.—Occurs only within the Appalachian Mountain chain, its marginal plateau and mountain balds from the Hudson River southwest through Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama (Fig. 11). The rabbit is presently distributed in discrete populations in the higher elevations and balds in a pattern similar to that of a refugial relict (Chapman & Stauffer 1981). A detailed range map of the type locality and the surrounding areas is presented in Chapman et al. (1977).

Diagnosis.—Medium-sized rabbit, with fine, silky fur. The upper sides are pinkish buff to ochraceous buff in color while the venter is bright whitish to pale buffy whitish, fore legs are rusty rufous. The cheeks have a distinct gray-grizzled appearance. The ears are short and rounded with the anterior edges covered with an edging of distinct black hair. There is usually a distinct black spot between the ears, and rarely a prominent white spot or blaze on the forehead (one example USNM 567191). Skull is grossly similar in appearance to that of *S. transitionalis.*

Comparisons.—*S. obscurus* differs from *S. transitionalis* in that the adult skull (length 65.5–75.2 mm) is proportionately shorter anteriorly (as reflected in the hard palate: palate vacuity ratio) and narrower medially (as reflected in the I^1 breadth: anterior frontal breadth and hard palate: anterior frontal breadth ratios) (Table 5). Nelson (1909:198) noted that specimens of *S. transitionalis* [*S. obscurus*] "with the heaviest skulls examined are from Alexandria, Virginia, and Travelers Repose, West Virginia."

The single specimen from Alexandria, Virginia, included in our preliminary investigations was found to behave inconsistently in both the univariate and multivariate analyses. This, coupled to its position well outside the ranges of either *S. transitionalis* or *S. obscurus,* as defined by this study, resulted in its exclusion from the 274 specimens comprising our final data set. The need for new material from this locality is clearly indicated both to ensure against incorrect species identification, as well as to determine possible relationship to other *Sylvilagus.* Additional sampling, especially in the New York area, is important to further delineate the distribution of these two species.

None of the pelage characteristics are clearly diagnostic for differentiating between *S. obscurus* and *S. transitionalis.* Furthermore, in the absence of cytogenetic data, which provides for the unequivocal identification of these sibling species, our data show that practical cranial delineation rests on the detection of subtle differences in the anterior and medial portions of the skull. Correct identification of specimens can be obtained using the results of the discriminant function analysis (see Table 3 for details).

Remarks.—The scientific name *S. obscurus* is given to this species because of its secretive and elusive behavior and its similar appearance to *S. transitionalis.* The common name Appalachian Cottontail refers to the distribution of the species which is wholly within the Appalachian Mountain chain. The type locality lies on the border between Grant and Tucker counties, West Virginia.

Specimens examined.—Holotype, allotype, paratypes and 86 specimens from localities listed below. The numbers following county names refer to the number of specimens examined from each locality.

Pennsylvania: Ulysses, Potter Co., 2 (CM);

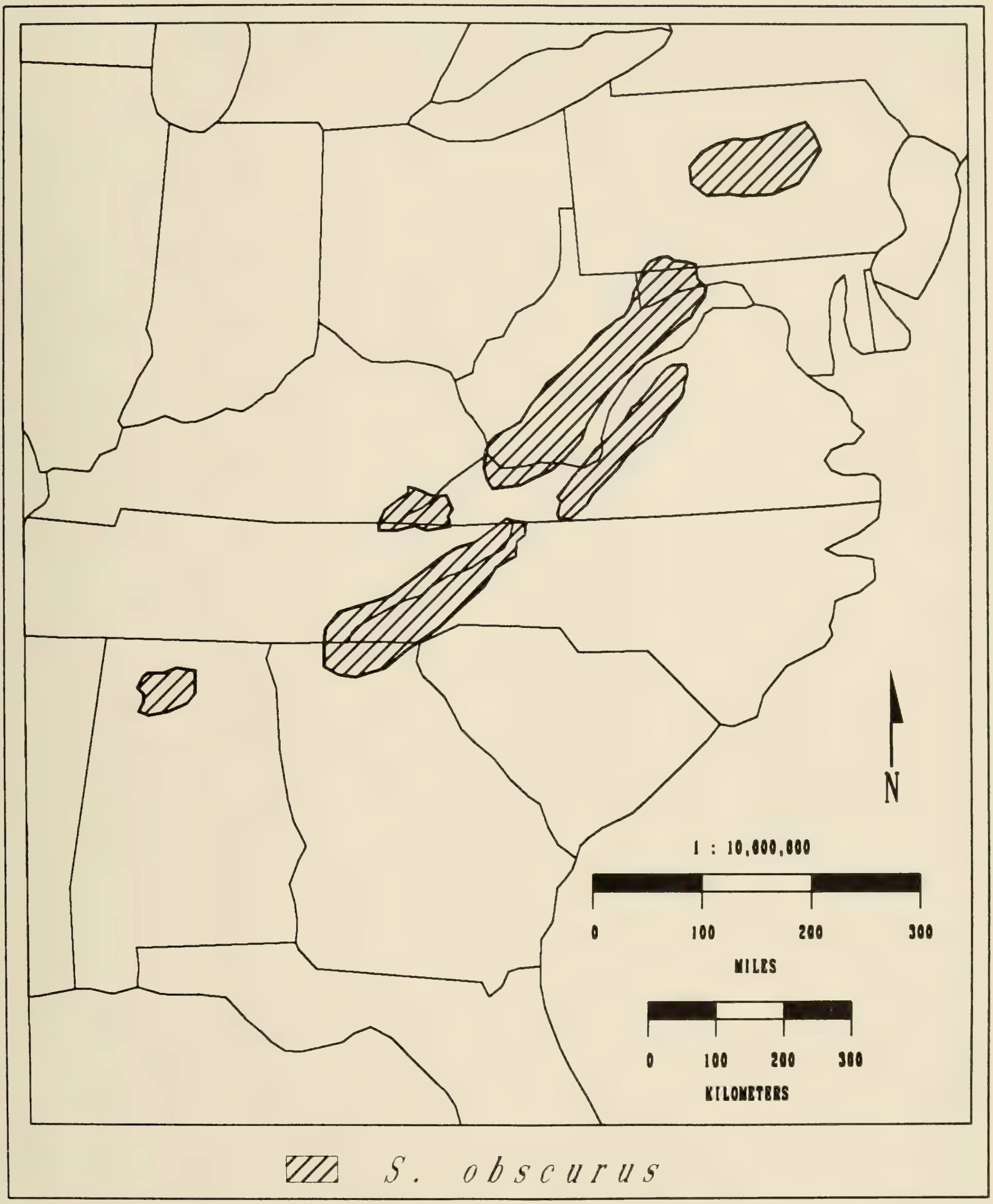

Fig. 11. Current distribution of *S. obscurus.* Distribution map based on this study and data collected by Chapman and Stauffer (1981).

Renovo, Clinton Co., 1 (USNM); White Haven, Luzerne Co., 1 (CM); Wingate, Centre Co., 1 (CM); Cashtown, Adams Co., 1 (CM); Powdermill Nature Preserve, Westmoreland Co., 1 (CM); Meyersdale, Somerset Co., 1 (CM); Markleysburg, Fayette Co., 1 (CM).

Maryland: Warnick Point, Garrett Co., 2

Table 5.—Variation in ratios calculated by contrasting selected measurements with high positive and negative loadings on Principal component II. Standard deviations estimates were based on a single sample comprising large numbers of specimens; *S. transitionalis* (OTU 14, $n = 65$) and *S. obscurus* (OTU 28, $n = 28$).

Ratio	*S. transitionalis*		*S. obscurus*	
Hard palate length × 100/ Palate vacuity length	Mean	35.82	Mean	32.70
	Max	43.04	Max	38.45
	Min	28.29	Min	27.58
	Mean + *SD*	38.46	Mean + *SD*	34.84
	Mean − *SD*	33.18	Mean − *SD*	30.56
	n	178.00	*n*	92.00
I^1 breadth × 100/ Palate vacuity length	Mean	15.89	Mean	14.86
	Max	17.83	Max	17.54
	Min	13.75	Min	12.80
	Mean + *SD*	16.59	Mean + *SD*	15.50
	Mean − *SD*	15.19	Mean − *SD*	14.22
	n	176.00	*n*	93.00
Hard palate length × 100/ Parietal length	Mean	40.65	Mean	37.20
	Max	48.09	Max	44.61
	Min	32.78	Min	27.49
	Mean + *SD*	43.44	Mean + *SD*	39.82
	Mean − *SD*	37.87	Mean − *SD*	34.57
	n	175.00	*n*	89.00
I^1 breadth × 100/ Anterior frontal breadth	Mean	18.57	Mean	16.18
	Max	21.31	Max	19.44
	Min	15.93	Min	13.48
	Mean + *SD*	19.73	Mean + *SD*	17.05
	Mean − *SD*	17.42	Mean − *SD*	15.32
	n	174.00	*n*	92.00
Hard palate length × 100/ Anterior frontal breadth	Mean	41.88	Mean	35.76
	Max	50.22	Max	46.09
	Min	31.14	Min	26.44
	Mean + *SD*	44.98	Mean + *SD*	38.24
	Mean − *SD*	38.79	Mean − *SD*	33.27
	n	176.00	*n*	91.00

(USNM); New Germany, Garrett Co., 5 (USNM); Elk Lick, Garrett Co., 6 (USNM); Savage River State Forest, Garrett Co., 2 (USNM); Popular Lick, Garrett Co., 7 (USNM); Meadow Mountain, Garrett Co., 1 (USNM); Finzel, Garrett Co., 1 (USNM); Garrett Co., 1 (USNM); Frostburg, Allegany Co., 1 (USNM).

West Virginia: Cacapon Mountain, Morgan Co., 1 (USNM); Dolly Sods, Grant Co., 16 (USNM), 1 (NC); Mt. Storm, Grant Co., 1 (USNM); Stony River Bridge, Route 50, Grant Co., 1 (USNM); Davis, Tucker Co., 4 (USNM); White Sulphur Springs, Greenbriar Co., 1 (USNM), 1 (CFM).

Virginia: Shenandoah National Park, Madison Co., 1 (USNM); Elliot Knob, Augusta Co., 2 (USNM); Newman's Run, Allegeheny Mountains, Highland Co., 3 (USNM); Mountain Lake, Giles Co., 1 (CFM); Sinking Creek Mountain, Montgomery Co., 1 (USNM); Haysi, Dickenson Co., 1 (USNM); Saltville, Smyth Co., 3 (USNM); Russell Co., 1 (USNM).

North Carolina: Roan Mountain, Mitchell Co., 3 (USNM).

South Carolina: Walhalla, Oconee Co., 1 (USNM).

Tennessee: Carvers Gap, Carter Co., 1 (USNM); Smoky Mountain Low Gap, Cocke Co., 1 (USNM).

Georgia: Young Harris, Towns Co., 2

(USNM); Brasstown Bald, Union Co., 1 (USNM).

Alabama: Ardell, Cullman Co., 1 (USNM); Flannigan Creek, Lawrence Co., 1 (USNM).

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Appendix I—Specimens Included in Analysis

The numbers preceeding each locality can be used to determine the geographic grouping of OTUs in the multivariate analysis (See Table 1).

Maine: (1) Gray, Cumberland Co.; (2) Cape Elizabeth, Cumberland Co.;

New Hampshire: (3) Enfield, Grafton Co.; (4) West Lebanon, Grafton Co.; (5) Newport, Sullivan Co.; (6) Lempster, Sullivan Co.; (7) Concord, Merrimack Co.; (8) Bow, Merrimack Co.; (9) Swanzey, Cheshire Co.; (10) Rindge, Cheshire Co.; (11) Walpole, Cheshire Co.; (12) Cold River, Cheshire Co.; (13) Hancock, Hillsborough Co.; (14) Manchester, Hillsborough Co.; (15) Nashua, Hillsborough Co.; (16) Greenville, Hillsborough Co.; (17) Litchfield, Hillsborough Co.; (18) Milford, Hillsborough Co.; (19) Somersworth, Strafford Co.; (20) Durham, Strafford Co.; (21) Windham, Rockingham Co.; (22) Greenland, Rockingham Co.;

Vermont: (23) Dorset, Bennington Co.; (24) Mendon, Rutland Co.; (25) Vernon Windham Co.; (26) Saxtons River, Windham Co.;

Massachusetts: (27) Rowe, Franklin Co.; (28) Birch Hill, Worcester Co.; (29) Royalston, Worcester Co.; (30) Wilmington, Middlesex Co.; (31) Dunstable, Middlesex Co.; (32) Shirley, Middlesex, Co.;

Rhode Island: (33) Wallum Lake, Providence Co.; (34) Arcadia, Washington Co.; (35) Exeter, Washington Co.; (36) North Kingston, Washington Co.; (37) Pettaquamscutt, Washington Co.; (38) Charleston, Washington Co.; (39) Worden Pond, Washington Co.; (40) Wolf Rock, Washington Co.; (41) Middlebridge, Washington Co.; (42) Richmond, Washington Co.; (43) Washington Co.;

Connecticut: (44) Westbrook, Middlesex Co.; (45) East Haddam, Middlesex Co.; (46) Killingsworth, Middlesex Co.; (47) Barn Island (Stonington), New London Co.; (48) Pawcatuck, New London Co.; (49) Niantic, New London Co.; (50) Ashford, Windham Co.; (51) Pomfret-Abington, Windham Co.; (52) Windham, Windham Co.; (53) Warrenville, Windham Co.; (54) Thomson, Windham Co.; (55) Putnam, Windham Co.; (56) Franklin, New London Co.; (57) Salem, New London Co.; (58) Woodstock, Windham Co.; (59) Lebanon, Windham Co.; (60) Mansfield, Tolland Co.; (61) Norwich, New London Co.; (62) Plainfield, New London Co.; (63) Chaplin, Windham Co.; (64) Westford, Windham Co.; (65) Sterling, Windham Co.; (66) Stonington, New London Co.; (67) Killingly, Windham Co.; (68) Storrs, Tolland Co.; (69) Waterford, New London Co.; (70) Stafford Springs, Tolland Co.; (71) Willington, Tolland Co.; (72) Amston-Hebron, Tolland Co.; (73) New Haven, New Haven Co.; (74) Milford, New Haven Co.; (75) Sharon Mountain, Litchfield Co.; (76) Macedonia Brook SP, Litchfield Co.; (77) Cornwall, Litchfield Co.; (78) Woodbury, Fairfield Co.; (79) Torrington, Litchfield Co.; (80) Canaan, Litchfield Co.; (81) Danbury, Fairfield Co.; (82) Fairfield, Fairfield Co.; (83) Fairfield, Larson Wildlife Sanctuary, Fairfield Co.; (84) Easton, Fairfield Co.; (85) North Granby, Hartford Co.; (86) Southbury, New Haven Co.;

New York: (87) Mastic, Suffolk Co.; (88) Hastings, Westchester Co.; (89) Sing-Sing, Westchester Co.; (90) Monticello, Sullivan Co.; (91) Lake George, Warren Co.;

Pennsylvania: (92) Ulysses, Potter Co.; (93) Renovo, Clinton Co.; (94) White Haven, Luzerne Co.; (95) Wingate, Centre Co.; (96) Cashtown, Adams Co.; (97) Powdermill Nature Preserve, Rector, Westmoreland Co.; (98) Meyersdale, Somerset Co.; (99) Markleysburg, Fayette Co.;

Maryland: (100) New Germany, Garrett Co.; (101) Hummel Farm, Garrett Co.; (102) Poplar Lick, Garrett Co.; (103) Elk Lick, Garrett Co.; (104) Savage River, Garrett Co.; (105) Meadow Mountain, Garrett Co.; (106) Frostburg, Garrett Co.; (107) Garrett Co.; (108) Warnick Point, Garrett Co.; (109) Finzel, Garrett Co.;

West Virginia: (110) Dolly Sods, Grant Co.; (111) Mount Storm, Grant Co.; (112) Stony River, Grant Co.; (113) Dolly Sods, Tucker Co.; (114) Davis, Tucker Co.; (115) Cacapon Mt, Morgan Co.; (116) White Sulphur Springs, Greenbriar Co.;

Virginia: (117) Shenandoah National Park, Madison Co.; (118) Elliot Knob, Augusta Co.; (119) Newman's Run, Allegeheny Mountains, Highland Co.; (120) Mountain Lake, Giles Co.; (121) Sinking Creek Mountain, Montgomery Co.; (122) Haysi, Dickenson Co.; (123) Saltville, Smyth Co.; (124) Russell Co.;

Tennessee: (125) Smoky Mountain Low Gap, Cocke Co.; (126) Carvers Gap, Carter Co.;

North Carolina: (127) Roan Mountain, Mitchell Co.;

South Carolina: (128) Walhalla, Oconee Co.;

Alabama: (129) Flannigan Creek, Black Warrior Wildlife Management Area, Lawrence Co.; (130) Ardell, Cullman Co.;

Georgia: (131) Young Harris, Towns Co.; (132) Brasstown Bald, Towns Co.;

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DISTRIBUTION, GEOGRAPHIC VARIATION, AND SYSTEMATIC RELATIONSHIPS WITHIN *NELSONIA* (RODENTIA: SIGMODONTINAE)

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Abstract.—Geographic differentiation within *Nelsonia neotomodon* was reviewed based on variation in mensural and pelage characters in *N. n. neotomodon, N. n. cliftoni,* and *N. n. goldmani,* from western México. Geographic variation within subspecies is minor and spatially unpatterned. Several pelage and cranial characters distinguish *N. n. neotomodon* to the northwest from both *N. n. cliftoni* and *N. n. goldmani* to the southeast. Notably, the zygomatic plate is narrow without an anteorbital zygomatic notch in *N. n. neotomodon,* whereas the plate is broad resulting in a distinct anteorbital notch in the southeastern taxa. Most geographic samples of *Nelsonia* probably represent allopatric populations and species boundaries cannot be determined objectively using the biological species concept. We hypothesize that two diagnosable monophyletic lineages occur within the genus and recognize them as species (*N. neotomodon* and *N. goldmani*) based on a phylogenetic species concept. The taxon *cliftoni* is arranged as a subspecies of *N. goldmani* based on cranial similarities but categorical differences in color of pelage. Biogeographic implications of the geographic distribution of *Nelsonia* and its spatial pattern of morphological differentiation are discussed.

Resumen.—Se revisaron las relaciones sistemáticas de *Nelsonia neotomodon,* considerando la variación en caracteres mensurables y del pelaje en *N. n. neotomodon, N. n. cliftoni* y *N. n. goldmani* del occidente de México. La variación geográfica dentro de las subespecies fue pequeña y sin un patrón espacial definido. Algunas características craneanas y del pelaje distinguieron a *N. n. neotomodon,* del noroeste, con respecto a *N. n. cliftoni* y a *N. n. goldmani* del sureste. Particularmente, la placa cigomática resultó angosta y sin una escotadura cigomática anterorbitaria en *N. n. neotomodon,* mientras que en los taxa del sureste la placa fue ancha y con una escotadura anterorbitaria evidente. La mayoría de las muestras estudiadas representan probablemente poblaciones alopátricas y, por tanto, los límites entre especies no pueden determinarse de manera objectiva utilizando el concepto biológico de especie. Nosotros proponemos la hipótesis de que existen dos linajes monofiléticos diagnosticables dentro del género y los reconocemos como especies (*N. neotomodon* y *N. goldmani*), utilizando el concepto filogenético de especie. Colocamos al taxón *cliftoni* como una subespecie de *N. goldmani,* basándonos en semejanzas craneanas pero considerando diferencias categóricas en el color del pelaje. Se discuten las implicaciones biogeográficas de la distribución de *Nelsonia* y su patrón espacial de diferenciación morfológica.

The diminutive woodrat, *Nelsonia neotomodon,* is currently viewed as a monotypic genus of neotomine-peromyscine rodent, and occurs at scattered montane localities in the southwestern Sierra Madre Occidental and western portion of the Transvolcanic Sierra of west-central México (Fig. 1). *Nelsonia* is seldom common and is confined to isolated cool, mesic coniferous, pine-oak, and mesophytic 'cloud' forests, usually on rocky cliff - or hillsides, at elevations above 2000 m (Hooper 1954, Genoways & Jones 1968). The genus is of considerable phylogenetic interest because it retains several primitive morphological characteristics which ally it phenetically with peromyscines (Hooper & Musser 1964, Carleton 1980); however, several synapomorphic characters identify it as a basal neotomine (Carleton 1980). *Nelsonia n. neotomodon* retains a karyotype similar to that hypothesized as primitive for peromyscine rodents (Engstrom & Bickham 1983).

Nelsonia neotomodon was described by Merriam (1897) based on specimens taken in the Sierra Madre Occidental of Jalisco and Zacatecas. Peculiarities of the skull and teeth distinguished the new genus from both *Neotoma* and *Peromyscus.* Later, Merriam (1903) described a second species, *N. goldmani,* based on specimens collected in the western Transvolcanic Sierra of Michoacán. Compared to *N. neotomodon,* this form was darker in color, lacked a white-tipped tail, and had a distinct anteorbital notch in the zygomatic process of the maxilla. Hooper (1954) reported additional specimens from Aguascalientes and Durango, reviewed geographic variation within the genus, and synonymized the two taxa, regarding them as intergrading subspecies of *N. neotomodon.* Genoways & Jones (1968) described a third subspecies, *N. n. cliftoni,* from specimens collected on El Nevado de Colima at the western edge of the Transvolcanic Sierra in Jalisco. This subspecies was intermediate in dorsal coloration between the two previously recognized taxa, but most closely resembled *N. n. goldmani* in cranial traits. Additional specimens of *N. n. neotomodon* from Durango and Zacatecas were reported by Baker & Greer (1962), Engstrom & Bickham (1983), and Matson & Baker (1986). Glendinning (1992) recently collected a specimen of *N. n. goldmani* from eastern Michoacán. The purposes of this paper are to report additional distributional records of *Nelsonia* and to reassess morphological variation within the genus based on material accumulated since Hooper's (1954) synopsis.

Materials and Methods

We examined a total of 62 specimens in the morphological analyses. Specimens examined are listed under the synonymies of taxa, and institutions housing those specimens are as follows: Florida Museum of Natural History, University of Florida (UFMNH); Museum of Natural History, University of Kansas (KU); Natural History Museum of Los Angeles County (LACM); The Museum, Michigan State University (MSU); Texas Cooperative Wildlife Collections, Texas A&M University (TCWC); Museum of Zoology, University of Michigan (UMMZ); Instituto de Biología, Universidad Nacional Autónoma de México (UNAM); National Museum of Natural History (USNM).

We assigned specimens to one of five presumptive age classes (1–5, from youngest to oldest) as described by Hoffmeister & de la Torre (1960), based on degree of eruption and wear of the upper molars, except that we divided their Group 4 (old adults) into two groups. In our toothwear class 4, the re-entrant folds of enamel on M^1 as seen laterally were present but short, and did not extend fully to the midpoint between the occlusal surface and alveolus; in our toothwear class 5, the re-entrant folds of enamel were only barely visible or entirely absent when viewed laterally, due to extensive wear on the occlusal surface.

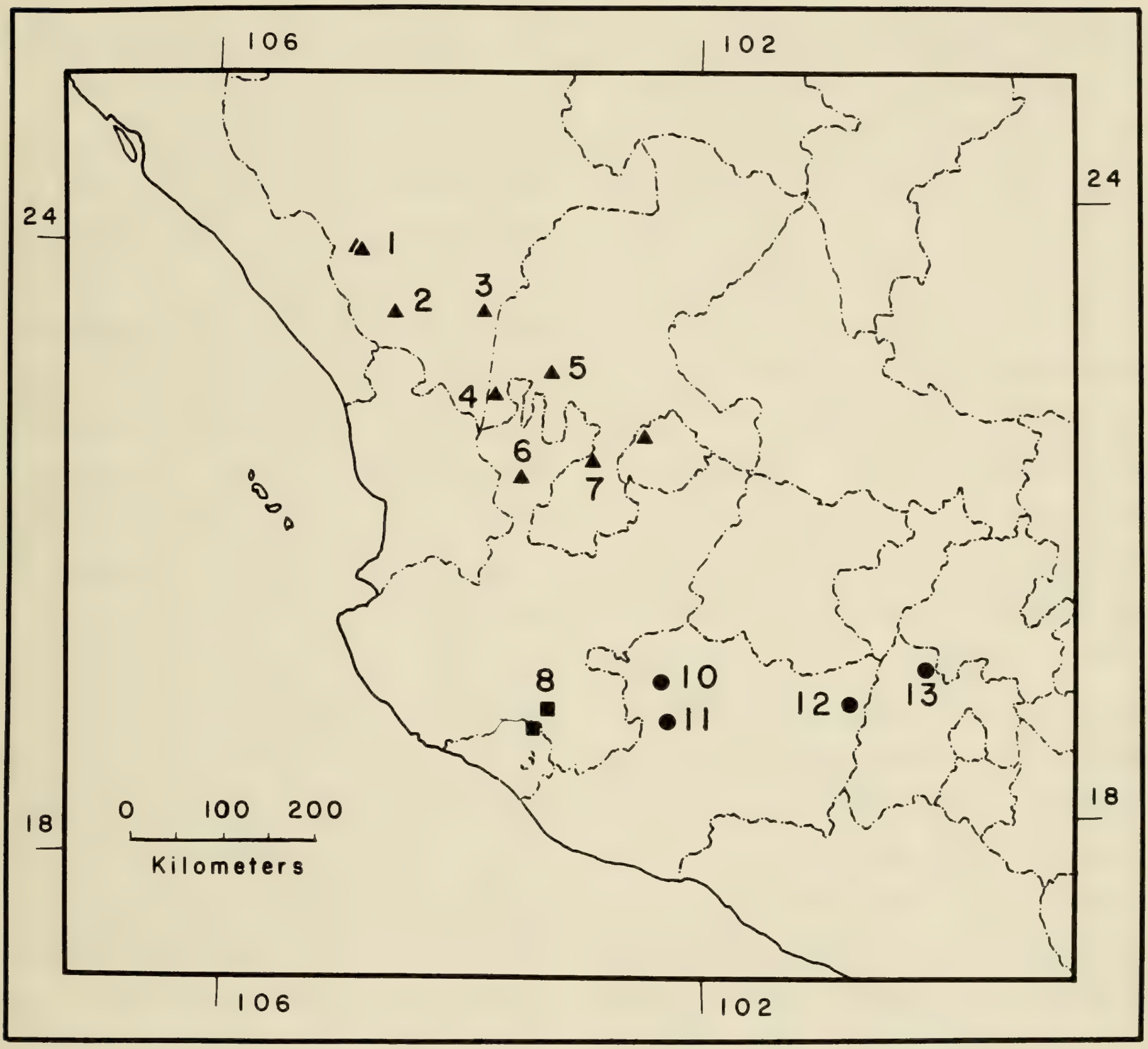

Fig. 1. Map of west-central México showing the distribution of *Nelsonia neotomodon* and location of samples used in the analysis of geographic variation. Symbols represent locality records of subspecies as follows: solid triangle = *N. n. neotomodon*; solid square = *N. n. cliftoni*; solid circle = *N. n. goldmani*. Numbered samples were used in the statistical analyses of geographic variation and are defined in text.

For each specimen, we recorded the following four external (from specimen labels) and 16 cranial measurements (taken to the nearest 0.1 mm using dial calipers) as defined by Hooper (1952) and Genoways (1973) except where indicated: total length (TL), length of tail (LT), length of hind foot (LHF), length of ear (LE), greatest length of skull (GLS), zygomatic breadth (ZB), postorbital constriction (POC), length of rostrum (LR), breadth of rostrum (BR), mastoid breadth (MB), length of interparietal (LIP), width of interparietal (WIP), breadth of zygomatic plate (BZP), length of palate (LP), length of maxillary toothrow (LMT), breadth across molars (BM; greatest width between labial borders of the second upper molars), length of auditory bulla (LAB; greatest length from posterior border of auditory bulla to anterior border, excluding length of eustachian tube), width of auditory bulla (WAB; greatest width from medial groove formed by carotid canal to the groove formed by the laterodorsal border of the auditory bulla), post-dental palatal width (PPW; least width across constriction of maxillaries posterior to the third upper molars and anterior to the lateral pterygoid fossa), depth of skull (DS; taken following Rogers & Schmidly 1982).

Because so few specimens of *Nelsonia* are available, we initially grouped all specimens of *N. n. neotomodon* (n = 30) as a single sample to estimate overall effects of age and sex on external and cranial dimensions. Variation within this sample was analyzed to determine if sexes and some toothwear classes were statistically homogeneous and could be pooled in analyses of geographic variation. Results should be considered approximate because overall sample size was small and individuals were grouped over a wide geographic area (Durango to Jalisco) over which intersample variation most likely occurs. Significance of the effects of age, sex, and interaction between these factors was tested using a two-way analysis of variance (*ANOVA*) considering both sex and toothwear class as fixed factors. A posteriori, Tukey-Kramer multiple range tests were used to identify statistically homogeneous subsets of age classes. We also estimated the percentage contribution of sex, age, and interaction to within-sample variation by variance partitioning of a two-way *ANOVA* considering sex and age as random factors (Leamy 1983). Because the main effects (sex and age) were not independent, variance partitioning was performed once with age entered first into the model and once with sex entered first. Estimates of variance components differed by 1% or less when order of the main effects was altered and only results with sex entered first are presented.

Because of the discontinuous distribution of *Nelsonia,* many sampled populations likely are allopatric. In the analysis of geographic variation, we separated most samples, rather than group localities among which gene flow was unlikely. Consequently, several geographic samples consist of only one or a few individuals. Specimens were assigned to one of 13 geographic samples (Fig. 1) with reference to specific placenames and current (or presumed) subspecific assignment as follows (analytical sample sizes in parentheses): *N. n. neotomodon.*—Sample 1: Durango; San Luís, Cerro Huehuento (9). Sample 2: Durango; Revolcaderas (4). Sample 3: Durango; Vicente Guerrero (1). Sample 4: Zacatecas; Sierra Madre (4). Sample 5: Zacatecas; Valparaiso (2). Sample 6: Jalisco; Bolaños (3). Sample 7: Zacatecas; Plateado (3). *N. n. cliftoni.*—Sample 8: Jalisco; Jazmín (7). Sample 9: Colima; Volcán de Colima. Jalisco; Volcán de Fuego (8). *N. n. goldmani.*—Sample 10: Michoacán; Patambán (5). Sample 11: Michoacán; Tancitaro (3). Sample 12: Michoacán; Angangueo (1). Sample 13: México; Dexcaní El Alto (1).

The null hypothesis of homogeneity of means among geographic samples of each character was tested using one-way *ANOVA*. Variance components attributable to the nested effects of subspecific assignment, geographic locality within subspecies, and residual variation were estimated for each character from a two-level nested *ANOVA*. Subspecific assignment and locality are more properly considered fixed than random effects, and results of this analysis are only rough estimates. All univariate analyses were performed using routines of the Statistical Analysis System (SAS; SAS Institute, Inc. 1982).

Phenetic relationships among geographic samples were assessed using multivariate programs in the Numerical Taxonomy System (NTSYS PC 1.5; Rohlf 1988). Principal components analysis (PCA) was performed on the among sample variance-covariance matrix calculated from log-transformed means (or individual values) of geographic samples. Scores for each sample were plotted on the first two component axes to depict the among sample variation relative to the total variation. A minimum spanning tree (MST) was calculated from a taxonomic distance matrix and superimposed on the PCA plot to locate local distortion of distances between nearest neighbors resulting from plotting only two component axes.

Results

As part of an ecological study of rodents, one of us (OSH) collected two specimens of *Nelsonia* at Cañada de la Ermita, near Dexcaní El Alto in the state of México, a locality which extends the known range of the genus approximately 300 km to the east. Cañada de la Ermita is a deep canyon located on the northern slopes of the central portion of the Transvolcanic Sierra. There, large boulders shape the mouth of a steep ravine, the upper portions of which are covered by xerophytic vegetation such as cacti, century plants (*Agave* sp.), and several species of grasses. The height of the boulders secludes the lower reaches of the canyon which, coupled with the presence of a small spring at the bottom of the ravine, maintains much higher humidity in the gorge than above. Within the ravine, the vegetation consists of relictual, montane mesophytic 'cloud' forest characterized by the trees *Ilex tolucana, Cornus disciflora,* and *Garrya laurifolia* (Rzedowski 1969). Within this forest, there are also small stands of *Abies* sp., *Arbutus* sp., and scattered *Buddleia americana.* Epiphytic orchids and bromeliads (*Tillandsia usneoides*) adorn the branches of some trees. The understory is dominated by *Phytolacca* sp. which forms a dense, shrubby layer during the rainy season.

Diminutive wood rats were captured on the moist, north-facing slope within this relictual cloud forest, in areas of dense, year-round cover. One male was caught in a Sherman live-trap set near the base of a tree and a second was captured in a live-trap set beneath rocks within dense herbaceous cover. The tail of a third individual was found in a snap trap set approximately 2.5 m high on the trunk of an *Arbutus,* indicating that *Nelsonia* at least occasionally climb trees. The first specimen was collected on 26 August 1982 and had scrotal testes, whereas the second, collected on 17 March 1986, had inguinal testes measuring 9 mm in length. To identify these individuals to subspecies, we examined most available specimens of *Nelsonia,* including holotypes of all described taxa, prompting this review of geographic variation and systematic relationships.

In the two-way *ANOVA* tests of within sample variation in *N. n. neotomodon,* no character mean differed significantly between the sexes. The effect of age was significant ($P < 0.05$) for two of four external (TL, LT) and eight of 16 cranial measurements (BR, BZP, GLS, ZB, LR, MB, PPW, BM). For all cranial measurements (but not for either external character) in which the effect of age was significant, toothwear class 1 (juveniles) was significantly smaller than presumptive age classes with more advanced toothwear. Toothwear class 5 (old adults) averaged larger than other classes for all characters which differed significantly with age except PPW, although these differences were not significant by a posteriori multiple range tests. Interaction between sex and age was significant ($P < 0.05$) for post-dental palatal width. If sex and age are considered random factors (Leamy 1983), estimates of the percentage of variance attributable to sex averaged 2.0%, age 27.4%, interaction 8.1%, and residual variation (error) 62.5%, for all characters across the five toothwear classes (Table 1).

A second two-way *ANOVA* examining the main effects of sex and age was performed, including only toothwear classes 2 to 4. As in the previous analysis, no character differed significantly between sexes. The effect of age was significant for two external (TL, LT) and two cranial measurements (ZB, BM) and the effect of interaction between sex and age was significant for post-dental palatal width. Variance components estimated from the two-way *ANOVA* restricted to toothwear classes 2 to 4 averaged 3.5% for sex, 12.6% for age, 10.7% for interaction, and 73.2% for residual variation for all characters. For those characters in which the

Table 1.—Percentage of total variance attributable to sex (S), age (A), sex by age interaction (S × A), and error (E) for 20 external and cranial measurements in toothwear classes 1 to 5 and 2 to 4 in *Nelsonia neotomodon neotomodon*. Abbreviations of measurements are defined in text.

	Variance components							
	S	A	S × A	E	S	A	S × A	E
Measurement	(1–5)				(2–4)			
TL	0.0	62.9	0.0	37.1	0.0	59.3	0.0	40.7
LT	0.6	41.9	0.0	57.5	2.8	40.7	0.0	56.5
LHF	0.0	18.8	0.0	81.2	0.0	27.5	0.0	72.5
LE	7.3	25.6	0.0	67.1	7.2	28.3	0.0	64.5
GLS	0.0	73.4	9.8	16.8	0.0	0.0	36.6	63.4
ZB	0.0	61.9	0.0	38.1	0.0	47.3	0.0	52.7
POC	11.9	5.7	0.0	82.4	6.9	0.0	0.0	93.1
LR	0.0	47.4	8.8	43.8	9.8	0.0	16.0	74.2
BR	0.0	31.5	13.6	54.9	7.4	0.0	16.8	75.8
MB	0.0	51.5	0.0	48.5	5.1	4.1	0.0	90.8
LIP	0.0	0.0	14.5	85.5	0.0	0.0	14.5	85.5
WIP	2.1	1.3	0.0	96.6	1.9	1.6	0.0	96.5
BZP	0.0	20.7	14.8	64.5	0.0	0.0	19.8	80.2
LP	0.0	0.3	0.9	98.8	0.0	1.9	4.1	94.0
LMT	0.0	36.5	0.0	63.5	0.2	11.2	0.0	88.6
BM	0.0	55.6	12.4	32.0	0.0	29.5	19.0	51.5
LAB	3.8	8.0	0.4	87.8	15.3	0.0	0.4	84.3
WAB	0.0	0.0	32.1	67.9	0.0	0.0	32.1	67.9
PPW	0.0	0.0	55.1	44.9	0.0	0.0	55.0	45.0
DS	13.6	5.2	0.0	81.2	13.4	1.1	0.0	85.5
Mean	2.0	27.4	8.1	62.5	3.5	12.6	10.7	73.2

effect of age was significant across the restricted set of toothwear classes (TL, LT, ZB, BM), the estimated variance component attributable to age averaged 44.2% (Table 1).

As in most neotomine-peromyscine rodents, secondary sexual variation accounts for only a minor component of variance in external and cranial dimensions in *Nelsonia,* and sexes were pooled in subsequent analyses of geographic variation. One-half of the characters measured exhibited significant ontogenetic changes associated with advancing toothwear, most of which were attributable to increase in size between toothwear classes 1 and 2 and to a lesser degree between classes 4 and 5. The distribution of toothwear classes and presumed age structure among geographic samples of *Nelsonia* was heterogeneous. To avoid obscuring patterns of geographic variation by comparing samples with different composition of age groups, individuals of toothwear classes 1 and 5 were deleted from geographic samples.

In the analysis of geographic variation, one of four external (LHF) and 11 of 16 cranial measurements (GLS, ZB, POC, BR, BZP, PPW, LR, MB, DS, WIP, BM) were significantly heterogeneous ($P < 0.05$) among localities (Table 2). For those characters which exhibited significant interlocality effects, subspecific assignment accounted for an average of 24.8% of the total variance, variation among localities within subspecies an average of 15.6%, and residual variation an average of 59.6%. For two measurements (BZP, WIP), the majority of variance was attributable to subspecific assignment ($\bar{X} = 75.7\%$), and these characters primarily distinguished samples of *N. n. neotomodon* from *N. n. goldmani* and *N. n.*

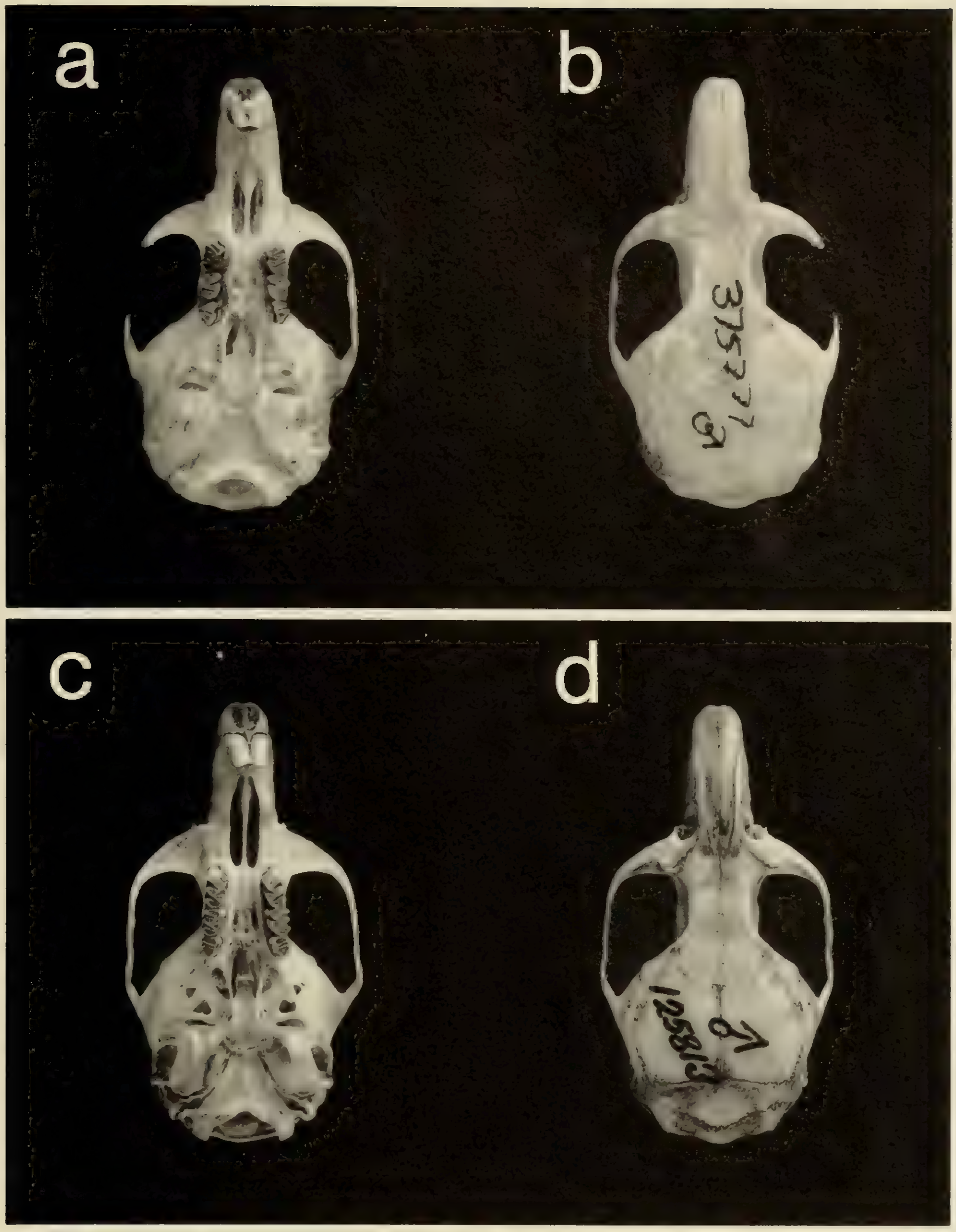

Fig. 2. Ventral and dorsal views, respectively, of the crania of: (a, b) an adult male *Nelsonia neotomodon neotomodon* from 3.5 mi E Revolcaderas, Durango (USNM 375777); and (c, d) an adult male *N. n. goldmani* from Mt. Tancitaro, Michoacán (USNM 125813). Note that a distinct notch is present in the anterior zygoma of *N. n. goldmani* (d) but absent in *N. n. neotomodon* (b).

cliftoni. As noted by Merriam (1903) and Hooper (1954), *N. n. neotomodon* can be distinguished from *N. n. goldmani* (and the more recently described *N. n. cliftoni*) by breadth of zygomatic plate and corresponding degree of development of the zygomatic notch (Fig. 2). For this character, there is a slight increase in size from north to south within *N. n. neotomodon,* which nevertheless retains a relatively narrow zygomatic plate and lacks a zygomatic notch in all populations. A pronounced difference in this character exists between *N. n. neotomodon* to the northwest and *N. n. cliftoni* and *N. n. goldmani* to the southeast, wherein the southeastern subspecies are characterized by a relatively broad zygomatic plate and distinct zygomatic notch. A similar pattern is evident in width of interparietal, wherein the interparietal is relatively narrow on average in *N. n. neotomodon,* and relatively broad on average in *N. n. cliftoni* and *N. n.*

Table 2.—Geographic variation in 12 external and cranial measurements in *Nelsonia.* Subspecific assignment of samples are: 1–7, *N. neotomodon neotomodon*; 8–9, *N. n. cliftoni*; 10–13, *N. n. goldmani.* Geographic localities of sample numbers are defined in text. Asterisks following *f*-statistics denote level of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Sample	*n*	Mean (range) ± 2 *SE*	Sample	*n*	Mean (range) ± 2 *SE*
		Length of hind foot			Greatest length of skull
1	9	26.4 (26.0–27.0) ± 0.35	1	8	32.1 (31.5–32.8) ± 0.38
2	4	25.8 (25.0–26.0) ± 0.50	2	4	31.6 (31.3–31.8) ± 0.21
3	1	26.0	3	1	31.9
4	4	28.5 (27.0–29.0) ± 1.00	4	4	32.1 (31.2–32.8) ± 0.69
5	2	27.5 (26.0–29.0) ± 3.00	5	2	32.5 (32.5–32.6) ± 0.05
6	3	29.3 (29.0–30.0) ± 0.67	6	2	32.5 (32.4–32.6) ± 0.20
7	3	29.0	7	3	32.6 (32.3–33.0) ± 0.41
8	7	28.0 (27.0–29.0) ± 0.61	8	6	32.5 (31.5–34.1) ± 0.78
9	8	26.8 (25.0–28.0) ± 0.63	9	7	32.0 (31.1–33.3) ± 0.65
10	5	29.2 (28.0–30.0) ± 0.75	10	5	31.0 (30.3–31.6) ± 0.52
11	3	29.3 (28.0–30.0) ± 1.33	11	3	32.4 (32.1–32.7) ± 0.35
12	0	—	12	1	33.4
13	1	25.0	13	1	32.6
		f = 10.84***			*f* = 2.30*
		Zygomatic breadth			Postorbital constriction
1	9	16.3 (15.7–16.9) ± 0.22	1	9	4.5 (4.4–4.7) ± 0.05
2	4	16.8 (15.9–17.3) ± 0.60	2	4	4.5 (4.3–4.7) ± 0.15
3	1	16.5	3	1	4.7
4	4	16.9 (16.6–17.8) ± 0.57	4	4	4.6 (4.4–5.1) ± 0.31
5	2	16.7 (16.6–16.9) ± 0.35	5	2	4.7 (4.6–4.8) ± 0.25
6	3	17.3 (17.2–17.5) ± 0.20	6	3	4.8 (4.7–4.9) ± 0.13
7	1	16.9	7	3	4.7 (4.6–4.8) ± 0.13
8	7	17.3 (16.1–18.4) ± 0.61	8	7	4.9 (4.7–5.0) ± 0.07
9	8	16.5 (15.8–17.0) ± 0.25	9	8	4.6 (4.4–4.8) ± 0.09
10	5	16.3 (15.8–16.8) ± 0.36	10	5	4.6 (4.4–4.8) ± 0.16
11	3	17.2 (17.1–17.4) ± 0.14	11	3	4.7 (4.6–4.8) ± 0.14
12	1	17.9	12	1	4.8
13	1	17.3	13	1	4.8
		f = 2.96**			*f* = 3.08**
		Breadth of rostrum			Breadth of zygomatic plate
1	9	4.9 (4.7–5.1) ± 0.08	1	9	2.8 (2.6–3.0) ± 0.08
2	4	4.9 (4.6–5.2) ± 0.26	2	4	2.8 (2.7–3.0) ± 0.10
3	1	5.1	3	1	2.7
4	4	5.0 (4.9–5.1) ± 0.10	4	4	2.9 (2.8–3.1) ± 0.10
5	2	5.1 (5.0–5.1) ± 0.05	5	2	3.0 (2.9–3.0) ± 0.05
6	3	5.3 (5.2–5.4) ± 0.10	6	3	3.1 (3.0–3.1) ± 0.06
7	3	4.8 (4.7–4.9) ± 0.09	7	3	3.0 (2.9–3.1) ± 0.12
8	7	5.2 (4.9–5.8) ± 0.24	8	7	3.4 (3.0–3.8) ± 0.18
9	8	5.0 (4.9–5.3) ± 0.13	9	8	3.4 (3.1–3.7) ± 0.13
10	5	5.1 (4.9–5.3) ± 0.14	10	5	3.3 (3.2–3.6) ± 0.12
11	3	5.3 (5.2–5.4) ± 0.14	11	3	3.4 (3.3–3.6) ± 0.20
12	1	5.1	12	1	3.3
13	1	5.3	13	1	3.4
		f = 2.19*			*f* = 11.58***
		Post-dental palatal width			Length of rostrum
1	9	5.1 (4.9–5.4) ± 0.11	1	9	12.8 (12.0–13.3) ± 0.27
2	4	5.0 (4.8–5.4) ± 0.31	2	4	12.3 (11.7–12.7) ± 0.49

Table 2.—Continued.

Sample	*n*	Mean (range) ± 2 *SE*	Sample	*n*	Mean (range) ± 2 *SE*
3	1	5.2	3	1	13.0
4	4	5.3 (5.2–5.4) ± 0.09	4	4	12.7 (12.1–13.3) ± 0.61
5	2	5.1 (5.0–5.1) ± 0.05	5	2	12.9 (12.6–13.2) ± 0.60
6	3	5.2 (4.9–5.4) ± 0.32	6	2	12.9 (12.9–13.0) ± 0.50
7	3	5.2 (5.1–5.4) ± 0.14	7	3	13.1 (12.7–13.4) ± 0.37
8	7	5.3 (5.1–5.7) ± 0.13	8	6	13.1 (12.6–13.7) ± 0.37
9	8	5.2 (5.1–5.3) ± 0.35	9	7	12.9 (12.3–13.5) ± 0.35
10	5	5.5 (5.3–5.8) ± 0.18	10	5	12.0 (11.6–12.5) ± 0.29
11	3	5.5 (5.4–5.6) ± 0.09	11	3	12.5 (12.2–12.9) ± 0.41
12	1	5.3	12	1	13.2
13	1	5.1	13	1	13.1
		f = 3.17**			*f* = 2.50*
		Mastoid breadth			Depth of skull
1	8	13.1 (12.8–13.6) ± 0.19	1	8	10.2 (9.7–10.6) ± 0.20
2	4	13.2 (12.9–13.6) ± 0.31	2	4	10.1 (10.0–10.4) ± 0.19
3	1	13.4	3	1	10.5
4	4	13.4 (13.0–13.9) ± 0.36	4	4	10.3 (9.9–10.7) ± 0.35
5	2	13.2 (13.0–13.4) ± 0.40	5	2	10.4 (10.2–10.5) ± 0.30
6	3	12.9 (12.7–13.2) ± 0.28	6	3	10.6 (10.3–10.9) ± 0.35
7	3	13.2 (13.1–13.2) ± 0.03	7	3	10.5 (10.2–10.7) ± 0.32
8	7	13.6 (13.0–14.5) ± 0.35	8	7	10.6 (10.0–11.1) ± 0.32
9	8	13.1 (12.7–13.8) ± 0.23	9	8	10.3 (9.8–10.7) ± 0.53
10	5	13.1 (13.0–13.3) ± 0.14	10	5	10.6 (10.4–10.8) ± 0.29
11	3	13.6 (13.3–13.8) ± 0.34	11	3	11.0 (10.8–11.2) ± 0.25
12	1	14.1	12	1	10.5
13	1	13.5	13	1	10.6
		f = 2.21*			*f* = 2.19*
		Width of interparietal			Breadth across molars
1	7	10.3 (9.5–11.0) ± 0.28	1	5	6.1 (5.9–6.4) ± 0.16
2	4	9.9 (9.4–10.5) ± 0.47	2	4	6.2 (6.0–6.5) ± 0.23
3	1	10.4	3	1	6.5
4	4	10.2 (9.1–11.2) ± 0.89	4	4	6.4 (6.3–6.5) ± 0.07
5	2	10.3 (10.0–10.6) ± 0.55	5	2	6.3 (6.1–6.4) ± 0.35
6	3	10.6 (10.5–10.8) ± 0.19	6	2	6.6 (6.4–6.7) ± 0.30
7	3	10.2 (9.7–10.5) ± 0.51	7	3	6.4 (6.3–6.5) ± 0.12
8	7	11.3 (10.8–11.7) ± 0.28	8	7	6.3 (6.1–6.6) ± 0.13
9	8	11.1 (10.7–11.5) ± 0.18	9	8	6.0 (5.9–6.2) ± 0.09
10	5	11.4 (11.0–11.8) ± 0.29	10	5	6.1 (5.9–6.3) ± 0.13
11	3	11.8 (11.4–12.1) ± 0.40	11	3	6.6 (6.5–6.7) ± 0.12
12	1	10.2	12	1	6.6
13	1	10.6	13	1	6.4
		f = 6.25***			*f* = 5.60***

goldmani (Table 2). This trend is reversed, however, in easternmost specimens of *N. n. goldmani* (Samples 12 and 13) which have relatively narrow interparietals.

Multivariate analyses of geographic variation were restricted to nine, geographically variable cranial measurements (GLS, POC, BR, BZP, PPW, LR, MB, DS, WIP). Three additional geographically variable characters were deleted from these analyses because they were not available for all samples (LHF) or exhibited significant variation

Table 3.—Eigenvalues, cumulative percentage of total variation, and character loadings resulting from a Principal Components Analysis of selected cranial variables in *Nelsonia* (see Fig. 3). Abbreviations of characters are defined in text.

Statistics and characters	Principal components	
	I	II
Eigenvalue	10.9	2.1
% of total variance	71.3	84.8
GLS	0.04	−0.16
POC	0.14	−0.16
LR	0	−0.24
BR	0.21	−0.04
MB	0.08	−0.12
WIP	0.45	0.24
BZP	0.87	−0.10
PPW	0.19	0.11
DS	0.16	0.01

among toothwear classes 2 to 4 (ZB, BM). In the PCA, two geographic groups of samples separated along the first component axis which had high positive loadings for BZP and WIP (Table 3, Fig. 3). Samples of *N. n. cliftoni* and *N. n. goldmani* (Samples 8–13) had higher scores on this component and were separated from samples of *N. n. neotomodon* (Samples 1–7) which had lower scores. In the projection of samples on the first two PC axes (accounting for 71.3% and 13.4% of the total variance, respectively), Sample 6 of *N. n. neotomodon* from northwestern Jalisco appears intermediate between these groups based primarily on the north to south increase in breadth of the zygomatic plate within *N. n. neotomodon.* In the minimum spanning tree, however, Sample 6 was the nearest neighbor to Sample 5 from southwestern Zacatecas and grouped with *N. n. neotomodon* (Fig. 3). The MST branch length between Samples 5 and 6 was 0.024, whereas that between Samples 6 and 13 (*N. n. goldmani* from México) was 0.035. Sample 6 also lacks the distinct zygomatic notch characteristic of *N. n. cliftoni* and *N. n. goldmani.*

Discussion

The diminutive woodrat usually inhabits rocky situations in association with wet-montane pine, fir, and cloud forests at elevations above 2000 m in west-central México (Hooper 1954). Populations of *Nelsonia* likely were partially continuous during periods in the Pleistocene when cooler and wetter conditions occurred at lower elevations than at present (Toledo 1982). Currently, however, pockets of suitable habitat are patchily distributed (Rzedowski & McVaugh 1966), and gene flow probably is sporadic, or absent, among most populations represented by available samples. In the absence of substantial gene flow, divergence among populations might occur stochastically or through adaptation to local environmental conditions. Geographic trends in morphological characters would be evident only to the extent that trends occur in environmental variables to which local populations are adapted, or that historical phylogenetic patterns of divergence are represented in extant populations.

Because of the small size of most geographic samples, we did not examine correlations of environmental and morphological variation. *Nelsonia,* however, is a habitat specialist with a small geographic range, and we anticipate that local environments in which it occurs are broadly similar. Accordingly, most mensural characters either did not vary with geography or their largest variance component was attributable to residual variation following removal of the effects of geographic locality and subspecific assignment. In particular, mensural variation within subspecies and among southeastern populations assigned to *N. n. goldmani* and *N. n. cliftoni* was minor.

Despite the overall similarity of cranial size and shape among samples of *Nelsonia* (Hooper 1954), certain cranial and pelage characters exhibited a clear geographic pattern that delineated samples of *N. n. neo-*

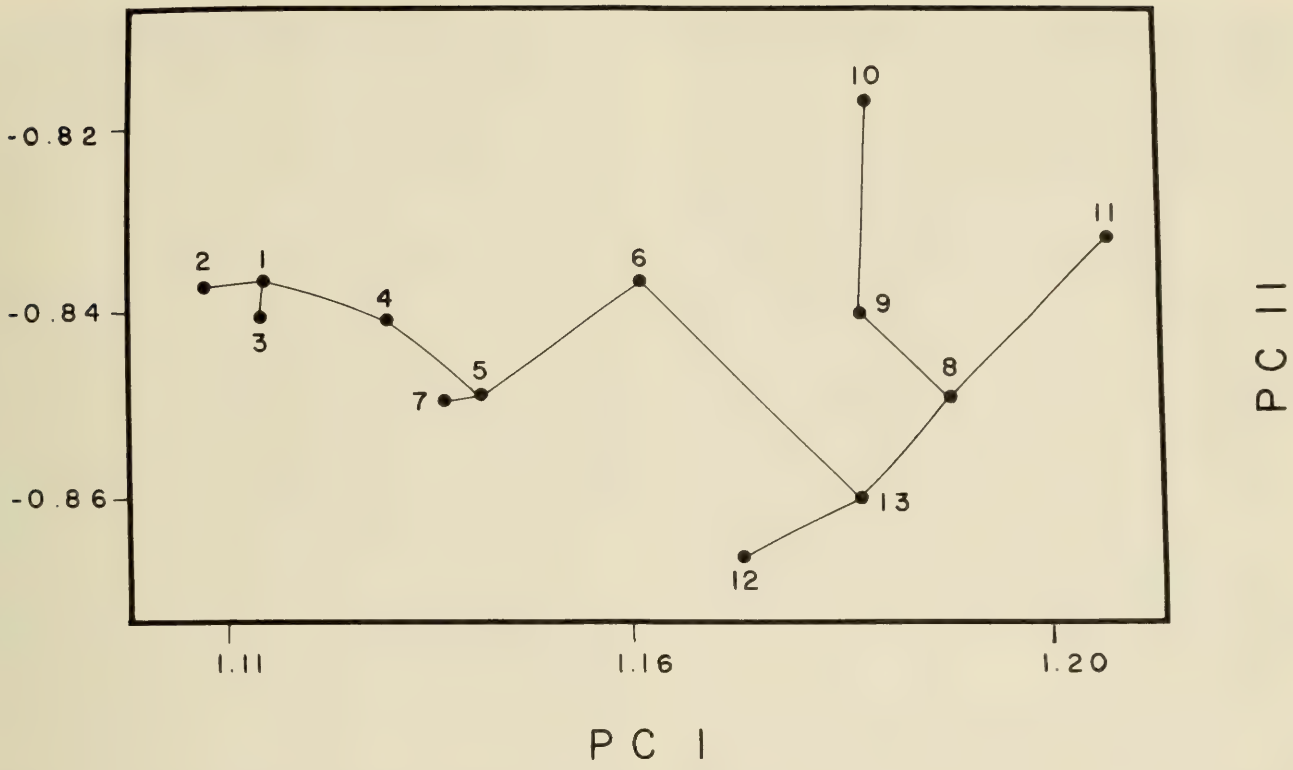

Fig. 3. Projections of geographic samples of *Nelsonia* onto the first two component axes resulting from a Principal Components Analysis of nine geographically variable cranial measurements. A minimum spanning tree is superimposed on the plot. Sample numbers are defined in text and illustrated in Fig. 1.

tomodon to the northwest from samples of *N. n. cliftoni* and *N. n. goldmani* to the southeast. Cranially, this step is most pronounced for breadth of the zygomatic plate and corresponding development of an anteorbital zygomatic notch. Samples of *N. n. neotomodon* have relatively narrow anterior zygoma and lack a zygomatic notch, and samples of *N. n. cliftoni* and *N. n. goldmani* have relatively broad anterior zygoma with a well-developed zygomatic notch (Fig. 2—see also Merriam 1903, Hooper 1954). Breadth of the zygomatic plate and concomitant development of the zygomatic notch in *Nelsonia* probably is correlated with the position of the anterior slip of the masseter lateralis muscle, which originates on the anterior, dorsal portion of the zygomatic plate (Rinker & Hooper 1950, Rinker 1954). In taxa with a distinct zygomatic notch, the anterior slip of the masseter lateralis is shifted forward and might be associated with changes in vectors of mastication or gnawing (Rinker & Hooper 1950). This character is relatively conservative in neotomine-peromyscine rodents, and we know of no other species that is polytypic for the presence/absence of a distinct zygomatic notch. Variation in this and several other characters was used to distinguish allopatric species of the peromyscine genus *Megadontomys* (Carleton 1989). Carleton (1980) coded the absence of a distinct notch as plesiomorphic for neotomine-peromyscines, and by this interpretation of polarity, the character state found in *N. n. goldmani* and *N. n. cliftoni* is derived.

Cranial differentiation within *Nelsonia* corresponds to variation in pelage color. Dorsal pelage of *N. n. neotomodon* is cinnamon-buff and darker dorsally than laterally; dorsal surfaces of the hind feet are usually white; and the tail is distinctly bicolored, usually with a white tip. In *N. n.*

goldmani, dorsal pelage is much darker with a distinct grayish cast and a fulvous but subdued lateral line; the hind feet are dusky, dorsally; the tail is indistinctly bicolor and lacks a white tip (Hooper 1954). Specimens of *N. n. cliftoni* are nearly intermediate in dorsal color, being decidedly darker than *N. n. neotomodon* but paler and more fulvous dorsally and laterally than *N. n. goldmani*; as in *N. n. goldmani,* the hind feet are dusky dorsally and the tail is usually indistinctly bicolor, lacking a white tip. In pelage characters, *N. n. cliftoni* most closely resembles *N. n. goldmani* but is categorically distinguishable from that taxon based on color of dorsal and lateral pelage (Genoways & Jones 1968).

Hooper (1954:5) stated that *N. n. neotomodon* and *N. n. goldmani* appeared to be "allopatric, intergrading forms" and arranged them as subspecies, although he did not discuss evidence for intergradation in detail. There is a north to south increase in breadth of the zygomatic plate in *N. n. neotomodon,* and the hind feet of a southeastern specimen of that taxon from Aguascalientes are slightly dusky; both characters appear to grade towards *N. n. goldmani.* The more recently described *N. n. cliftoni* appears intermediate in dorsal and lateral pelage color and is positioned geographically between the ranges of the other two taxa. In several cranial and pelage characters, however, there is a distinct gap between *N. n. neotomodon* and the two southeastern taxa with little evidence of recent intergradation. In particular, discrimination of these two groups is absolute based on the presence or absence of a zygomatic notch.

We hypothesize that divergence between northwestern and southeastern samples of *Nelsonia* is the result of historical disruption of gene flow and subsequent anagenesis, rather than local adaptation to current environmental conditions. We have no independent measure of genetic or phylogenetic relationships among populations within *Nelsonia.* Nonetheless, the discrete nature of the correlated pattern of cranial and pelage variation, the usual conservatism of development of the zygomatic notch within species of neotomine-peromyscines, and lack of compelling evidence of intergradation suggests that *N. neotomodon* represents a monophyletic lineage separate from *N. n. goldmani* and *N. n. cliftoni.* Demonstration of a lack of genetic divergence between *N. n. neotomodon* and the latter two taxa, or of increasing similarity of geographically intermediate populations in Aguascalientes and Jalisco, would refute this hypothesis.

Assuming that the two sets of allopatric populations of *Nelsonia* represent separate phylogenetic lineages, at what rank should they be classified? Conservative application of the biological species concept—that is "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970:12)—might dictate that these lineages be retained as subspecies within the polytypic *N. neotomodon,* until reproductive isolation and lack of intergradation is demonstrated convincingly. This species concept has been criticized, however, because it is not directly applicable to allopatric populations, relies on a primitive trait (ability to interbreed), and in formation of polytypic, allopatric species such as *N. neotomodon,* underestimates the number of distinct evolutionary units (Cracraft 1983, Donoghue 1985, McKitrick & Zink 1988). In the case of allopatric populations, a phylogenetic species concept provides an objective alternative and (in one formulation) defines species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983:170). Thus, by this definition, species are monophyletic lineages characterized by novel character states. Taken to an extreme using phyletically labile characters, this concept could result in recognition of trivial groups as distinct species. Interpreted conservatively, however, it provides an objective means of ranking allopatric populations and recognizes the maximum number of evolutionarily meaningful units as species. By this definition, we rank *goldmani* and *cliftoni* as a separate species (*N. goldmani*) from *N. neotomodon.*

The taxonomic status of *cliftoni* relative to *goldmani* is less clear. Genoways & Jones (1968) listed several cranial differences between these taxa, including (in *cliftoni*): more posterolateral orientation of auditory bullae; a shallower skull; larger average cranial measurements, especially greatest length of skull, zygomatic breadth, and length of rostrum; and a shorter maxillary toothrow relative to length of skull. The average toothwear class of the samples of *goldmani* from which Genoways & Jones (1968) drew their examples is 2.1, whereas the average toothwear class of their *cliftoni* samples is 3.0. Several of the reported cranial differences between these taxa are related to age and result from comparing younger samples of *goldmani* with older *cliftoni.* For example, the lateral direction of the posterior portion of the auditory bulla increases with age, and this character is nearly identical between the two taxa when individuals of the same toothwear class are compared. Specimens of *cliftoni* averaged larger than *goldmani* for greatest length of skull, zygomatic breadth, and length of rostrum, and smaller for depth of skull and length of maxillary toothrow, in accord with Genoways & Jones' (1968) description; however, only the difference in length of rostrum was significant. Although similar cranially, all specimens of *cliftoni* and *goldmani* can be distinguished easily based on color of dorsal and lateral pelage. We suggest that the discontinuous pattern of variation in pelage color between these taxa be recognized, while emphasizing the potential lability of these characters, by arranging *cliftoni* as a subspecies of *N. goldmani.*

The relictual, montane distribution of *Nelsonia* in the southern Sierra Madre Occidental (*N. neotomodon*) and in the extreme western (*N. g. cliftoni*) and west-central (*N. g. goldmani*) Transvolcanic Sierra corresponds to the Nearctic Distribution Pattern described for montane Middle American insects by Halffter (1987). This pattern includes Mexican taxa that occur in humid, temperate habitats at elevations above 1700 m, north of the Isthmus of Tehuantepec, and that have sister groups north of México (in this case *Neotoma*). In a vicariant biogeographic analysis of platynine beetles with this distribution pattern, Liebherr (1991) identified divergence between the Sierra Madre Occidental and more southerly mountain ranges (including the Transvolcanic Sierra) as the basal dichotomy in a general area cladogram. Endemic taxa of insects inhabiting these alternative basal areas exhibited a relatively distant cladistic relationship and usually were distinct at the level of species or higher. An apparent distributional hiatus for some of these taxa exists near the region of contact between the southern Sierra Madre Occidental and the western Transvolcanic Sierra in Nayarit and central Jalisco. There, elevations rarely exceed 2000 m and suitable wet-montane habitats are rare or absent (Genoways & Jones 1968, Halffter 1987).

In contrast to Hooper's (1954) interpretation of subspecific intergradation, a fundamental distinction among populations of *Nelsonia* also occurs between those occupying the Sierra Madre Occidental (*N. neotomodon*) and those in the Transvolcanic Sierra (*N. goldmani*). Diminutive woodrats have not been collected to date in the intervening region in Nayarit and central Jalisco. Correspondence to the Nearctic Distribution Pattern of Halffter (1987) implies that differentiation within *Nelsonia* results from the same vicariant events that fragmented distributions of other montane organisms of relatively low vagility. Halffter (1987) stated that taxa conforming to this distribution pattern likely originated in the Pliocene to Pleistocene, whereas Liebherr (1991) suggested that diversification of at least some of these taxa began earlier, in the

Miocene. Whatever the exact timing, divergence between *N. neotomodon* and *N. goldmani* probably is older than might be inferred from the relatively minor level of morphological divergence.

Synonymy and Specimens Examined

Nelsonia neotomodon Merriam

Nelsonia neotomodon Merriam, 1897:278 (17 Dec).

Nelsonia neotomodon neotomodon, Hooper, 1954:5 (17 Sep).

Specimens examined (30).—Aguascalientes: Sierra Fría, 8200 ft, 1 (UMMZ). Durango: east slope of Cerro Huehuento, 9500 ft, 1 (UMMZ); 1.5 mi W San Luis, 7550–8000 ft, 10 (6 MSU, 1 TCWC, 3 UMMZ); 6 mi NE Revolcaderas, 7800 ft, 1 (USNM); 3.5 mi E Revolcaderas, 7800 ft, 2 (USNM); 1 mi E Revolcaderas, 7300 ft, 1 (USNM); Rancho las Margaritas, 28 mi S, 17 mi W Vicente Guerrero, 8350 ft, 1 (MSU). Jalisco: Bolaños, 7600 ft, 3 (USNM). Zacatecas: Plateado [type locality, elevation between 7600 and 8500 ft, Hooper 1954:7], 3 (USNM); Sierra Madre, 8500 ft, 4 (USNM); 9 mi NW Valparaiso, 8350 ft, 1 (MSU); Valparaiso Mountains, 8700 ft, 2 (USNM).

Nelsonia goldmani goldmani Merriam

Nelsonia goldmani Merriam, 1903:80 (29 May).

Nelsonia neotomodon goldmani, Hooper, 1954:7 (17 Sep).

Specimens examined (15).—México: Cañada de la Ermita, 4 km N Dexcaní El Alto, 2 km S, 3.5 km E Jilotepec (19°56′N, 99°33′W), 2 (UNAM). Michoacán: Angangueo, Sierra Chincua, 3010 m, 1 (UFMNH); Patambán, 10,000 ft, 6 (USNM); Mt. Tancitaro, about 9500 ft, 4 (USNM); Mt. Tancitaro, about 9000 ft, 1 (USNM); Mt. Tancitaro, 1 (USNM) [type].

Remarks.—The specimens from México are the first recorded for that state.

Nelsonia goldmani cliftoni Genoways & Jones

Nelsonia neotomodon cliftoni Genoways & Jones, 1968:97 (30 Apr).

Specimens examined (17).—Colima: Volcán de Fuego, 9000 ft, 2 (LACM). Jalisco: 4 mi ENE Jazmín, 7700 ft, 1 (KU); 2.5 mi ENE Jazmín, 6800 ft [type locality], 6 (KU); Volcán de Colima, north slope Cerro Nevado, 8500 ft, 8 (LACM).

Remarks.—The specimens from Colima are the first recorded for that state.

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SEX AND AGE COMPONENTS OF VARIATION IN *PROECHIMYS CUVIERI* (RODENTIA: ECHIMYIDAE) FROM NORTHERN BRAZIL

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Abstract.—We examined non-geographic variation in 145 specimens of *Proechimys cuvieri* from northern Brazil and identified the proportion of total variation in seven external and 18 cranial measurements that was accounted for by differences in sex, and among ten age classes. The percent contribution of age to total variance was 16.6% for adults, 50.5% for juveniles, and 68.6% for all individuals combined. The contribution of variation due to sex was greater for adult age classes than for juveniles or for all individuals. Among adults, individual variation is great and may complicate analysis of geographic variation in this species. Males average larger than females, but not significantly so in most age classes and sexual dimorphism is marked in only one adult age class.

Spiny rats of the genus *Proechimys* display extensive morphological variation within and among populations that makes specific identification challenging and contributes to their taxonomic confusion (Thomas 1928, Martin 1970, Patton & Gardner 1972, Patton & Rogers 1983). *Proechimys* is one of the most abundant mammals in the Neotropical region but it is, nevertheless, one of the least-known (Patton 1987). Relationships within the genus are uncertain and require reexamination of most of its species (Reig et al. 1980).

Before we can define species boundaries and relations among species of *Proechimys,* we need to understand the sources of variation within populations and species and the contribution that each source of variation makes to the total variation. Specifically, as Straney (1978) noted, we need to understand non-geographic variation, which includes differences due to sex, age, and individual variation within a given population. Patton and Rogers (1983) examined variability due to age and sex for standard morphometric characters in *P. brevicauda.* One problem in such analyses is the small number of specimens available for study from a recognizable single taxon (Patton & Rogers 1983).

Our study was prompted by the availability of a relatively large sample of *P. cuvieri* from the Amazon forest region of northern Brazil, permitting us to study the sources of variation within one species. We analyzed non-geographic variation in this sample by recording the mensural changes that occur due to growth in 25 measurements of skin and skull and identifying the proportion of total variation in our sample that can be accounted for by differences in sex and among the identified age classes.

Methods

We examined 171 specimens of *Proechimys cuvieri.* Those with incomplete information were eliminated. Consequently, analyses are based on 145 specimens of *Proechimys cuvieri* from seven localities in Amapá State, northern Brazil (see Lara 1986). Species identification was based on the morphological characters given by Petter (1978) and Patton (1987), and by karyotype (see Reig et al. 1979, 1980) of a few specimens. Specimens are housed in the Museu Nacional do Rio de Janeiro (MN), and the National Museum of Natural History in Washington, D.C. (USNM).

Localities and numbers of specimens were: Brazil—Amapá State: Serra do Navio (114, MN; 26, USNM); Porto Platon (12, MN); Rio Tracajatuba (6, MN); Boa Fortuna do Rio Branco (2, MN); Vila Velha do Caciporé (2, MN); Vila Jornal (1, MN); Coração (3, USNM); no exact locality (5, MN). Serra do Navio (00°59′N, 52°03′W), Rio Tracajatuba (00°52′N, 50°58′W), Boa Fortuna do Rio Branco (00°47′N, 52°21′W), and Vila Jornal (00°54′N, 51°58′W) are in unflooded tropical evergreen rainforest. Vila Velha do Caciporé (03°20′N, 51°20′W) is a wetland with grasses and scattered low trees. Porto Platon (00°42′N, 51°27′W) and Coração (00°04′N, 51°10′W) are in savanna-like vegetation ("Cerrado") with distantly separated trees that range from 4 to 10 m in height. Such Cerrado habitat frequently is interspersed with wetlands. Precipitation in Amapá averages 2500–3300 mm/year.

The animals were classified according to the ten age classes of Patton & Rogers (1983), based on the sequence of tooth eruption and occlusal surface wear of molariform teeth. Due to the small number of younger animals in our sample, we combined age classes 2 and 3, and 5 and 6. Age class 1 is not represented in this study. Eighteen cranial measurements were taken to the nearest 0.05 mm, with dial calipers. Seven external measurements were recorded from specimen labels. Measurements, taken from Cockrum (1960) or otherwise defined, were head-body length (HBL); tail length (TL); hind foot length (HFL); length of hind foot with claw (HFC); length of ear from crown (EEH); length of ear from notch (IEH); weight (W); condylobasilar length (CBL; taken from anterior incisive alveolus to the posteriormost part of the occipital condyles); zygomatic breadth (ZB); basilar length (BSL); palatal length (PL; from posterior margin of incisive alveolus to the anterior margin of mesopterygoid fossa); left upper tooth row length (MTRL); maxillary breadth (MB); length of upper diastema (D); length of incisive foramen (IFL); breadth of incisive foramen at premaxillary-maxillary suture (IFB); width of tympanic portion of left auditory bulla (BLW); upper left incisor length (IL); width of upper incisors (IW); nasal length (NL); rostral breadth at maxillary-premaxillary suture (RB); least interorbital constriction (IOC); braincase breadth (BB; distance between the openings of the tympanic bullae); mandibular length (ML; from the posterior margin of the incisive alveolus to the right mandibular condyle); lower tooth row length (LTRL; from anterior alveolus of PM4 to posterior alveolus of M3).

We analyzed the data with standard descriptive analysis (SAS 1987) to obtain means and variances (Appendix 1). The General Linear Model procedure from SAS-PC (1987) was used to obtain the percentage contribution to total variance of age, sex, age by sex interaction, and error term for the 25 morphometric variables. The relative contribution of these four sources of variation were obtained by division of the sums of squares (SSQ) associated with each by the total SSQ. We assessed the contributions of each for all age classes (ages 2–10), just juveniles (ages 2–7) and just adults (ages 8–10). Leamy (1983) discussed techniques of variance partitioning and the advantages and disadvantages of the SSQ approach versus the variance component approach. The disadvantage of the SSQ technique is that for a given factor such as age, we cannot make strict comparison of its variation from one sample (i.e., all animals, only juveniles, only adults) to another because all samples do not have the same number of (age) classes or groups. Comparisons regarding general magnitude of differences are appropriate, however. The SSQ technique seemed to be the appropriate approach since it allows one to consider the overall mean plus the effect due to sex, age, the interaction term (age by sex) and the error term, instead of the overall mean plus some values due to sex and the other terms, as in the variance component approach.

Results and Discussion

We grouped the individuals from the seven localities into one sample to increase sample sizes for age and sex classes. The sizes of the separate samples precluded an analysis of geographic variation among them. Most of our specimens (114 of 145; 79%) come from a single locality. Consequently, there is little chance of undetected geographic variation confounding our analysis of this combined sample.

Variation among adults.—Among adult classes (8–10), age contributes an average of 16.59% to total variation. Sixteen of 25 variables showed significant variation due to the age term (Table 1). Sex contributed an average of 6.51% to the total variance with eleven of 25 variables varying significantly. Ten of these 11 variables are measurements of length (Table 1), the exception is braincase breadth. Sexual dimorphism in the skull apparently is related to elongation, rather than to width differences. Interaction between age and sex was low (mean = 2.51%). Only bullar width showed a significant interaction term.

A similar substantial age component and lack of sexual dimorphism has been found for the adults of other species of spiny rats. These include *P. albispinus* from northeast Brazil (Pessôa & Reis 1991), *P. brevicauda* from northern Peru (Patton & Rogers 1983), and *P. longicaudatus*-group member [erroneously identified as *guyannensis* by Martin (1970) and referred to by this name in the analysis of variation by Straney (1978); J. L. Patton, pers. comm.]. Variation of skull dimensions due to age was also found in three adult populations of *P. dimidiatus* from southeast Brazil (Pessôa & Reis 1990). The relatively large contribution of age to total variance, even among adults, may be characteristic of the genus (Patton & Rogers 1983). Nevertheless, despite the reported absence of sexual dimorphism in the mentioned studies of *P. brevicauda, P. longicaudatus*-group member, and *P. albispinus,* our sample exhibited sexual dimorphism. We cannot determine if this is a characteristic of *P. cuvieri* alone, or of this particular population from Amapá, because there are no other single population studies of *P. cuvieri* available for comparison.

Sexual dimorphism is most pronounced in age class 9. In this class, 12 out of 25 variables (HBL, HFL, HFC, CBL, BSL, PL, D, IFL, BLW, NL, BB, and ML) showed significant sexual dimorphism ($P < 0.05$). However, only three variables exhibited significant dimorphism in age classes 8 (HFL, HFC, and EEH) and 10 (HFL, HFC, and IOC). Sample sizes are adequate for examination in all three classes and thus do not account for the fact that one age class exhibits considerable sexual dimorphism, and the two adjacent age classes do not. Among adults, males are always larger than females, at any age. The general pattern is that adult males show a greater percentage change in size from age 8 to 9 whereas adult females show more change between ages 9 and 10 (Table 2, Fig. 1). The effect of this on an analysis of sexual dimorphism is that age class 9, the class showing greatest dimorphism, consists of males that have literally "jumped ahead" in growth compared to females of equivalent age (i.e., toothwear). Males are disproportionately larger than females only in this age class. One possible reason for the observed growth difference is the effect of reproductive activities (gestation and lactation) on females in age class 9. Animals of chronological age of six months are estimated to be in age class 6; animals 18 months of age, or older, would be in age classes 9–10 (Patton & Rogers 1983). Females of *P. brevicauda* show first evidence of breeding at age class 5 and 57% of females were pregnant or parous by age class 7 (Patton & Rogers 1983). By age class

Table 1.—Percent contribution to total variance of age, sex, interaction of age and sex, and error of 25 morphometric variables of *P. cuvieri*.

	All ages (2–10)				Juveniles (2–7)				Adults (8–10)			
Variable	Age	Sex	Age × sex	Error	Age	Sex	Age × sex	Error	Age	Sex	Age × sex	Error
HBL	71.88***	1.61**	0.67	21.09	58.34***	4.67*	0.62	36.06	19.53**	5.06*	2.62	70.99
TL	77.24***	0.42	0.18	21.21	68.00***	0.40	0.19	31.42	1.37	3.10	0.34	94.49
HFL	63.58***	3.83***	1.33	24.12	58.00***	2.06	1.36	37.98	2.70	31.17***	2.40	63.96
HFC	70.22***	3.29***	0.54	20.38	62.16***	2.93*	0.41	34.52	1.52	26.12**	1.53	70.52
EEH	19.69***	0.62	3.10	72.95	14.29	0.10	2.85	82.55	0.18	3.11	3.47	90.76
IEH	39.75***	1.28	3.92	52.33	25.60*	1.68	8.43	64.60	5.10	2.63	3.28	87.90
W	72.79***	0.96*	0.87	20.94	52.20***	6.01**	1.36	40.03	18.56	1.76	2.61	75.79
CBL	80.85***	1.58**	0.40	11.68	67.44***	3.41*	0.91	29.65	28.92***	10.51**	1.93	58.81
ZB	76.43***	0.94*	0.38	20.51	59.25***	3.93*	0.83	37.20	22.92**	0.86	0.23	76.10
BSL	79.34***	1.85***	0.67	10.99	66.23***	6.21**	0.84	27.54	33.93***	7.04**	4.19	53.53
PL	77.06***	0.88**	0.91	16.11	55.82***	0.62	1.20	42.28	30.00***	9.60**	3.21	55.18
MTRL	90.39***	0.09	0.57	5.26	81.69***	0.17	2.50*	15.08	0.82	2.75	2.11	93.53
MB	65.20***	0.86	1.92	28.53	11.60	2.92	7.62	78.95	36.26***	1.24	1.43	59.06
D	77.11***	1.54**	0.75	16.45	59.36***	2.44	2.18	36.35	30.43***	8.88**	1.42	59.28
IFL	55.49***	1.68*	0.78	37.25	41.53***	2.31	1.20	54.30	8.39*	5.14*	1.46	83.94
IFB	42.83***	1.12	2.07	51.81	22.85***	0.81	0.73	75.54	0.68	3.88	4.28	86.50
BLW	62.60***	2.05**	3.02	30.29	34.88***	5.25*	5.43	55.56	15.70**	3.23	6.80*	73.98
IL	67.09***	1.75**	1.39	27.79	35.88***	10.01**	3.02	52.63	22.08**	0.58	1.37	73.18
IW	77.22***	0.43	0.61	18.48	60.08***	0.59	1.45	38.16	22.68***	2.75	1.97	72.24
NL	77.20***	2.07***	0.59	14.52	65.47***	4.54**	0.99	30.32	14.38**	12.19**	2.65	70.74
RB	62.95***	2.09**	1.67	30.75	26.55**	6.88**	1.30	66.18	10.61*	3.11	5.70	79.67
IOC	66.45***	2.13**	1.54	29.28	45.01***	5.51**	1.93	49.15	16.35**	3.64	4.40	76.55
BB	78.52***	1.64**	0.54	16.70	58.88***	5.44**	2.02	35.08	28.68**	4.50**	1.15	66.57
ML	75.65***	1.28**	0.85	12.37	62.00***	1.95	1.68	27.26	37.63***	8.58**	3.21	47.49
LTRL	87.43***	0.49**	1.26**	8.31	69.69***	2.24*	4.65*	24.37	0.41	1.32	1.96	95.32
Mean	68.60	1.46	1.22	24.80	50.51	3.32	2.23	44.11	16.59	6.51	2.51	73.44

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

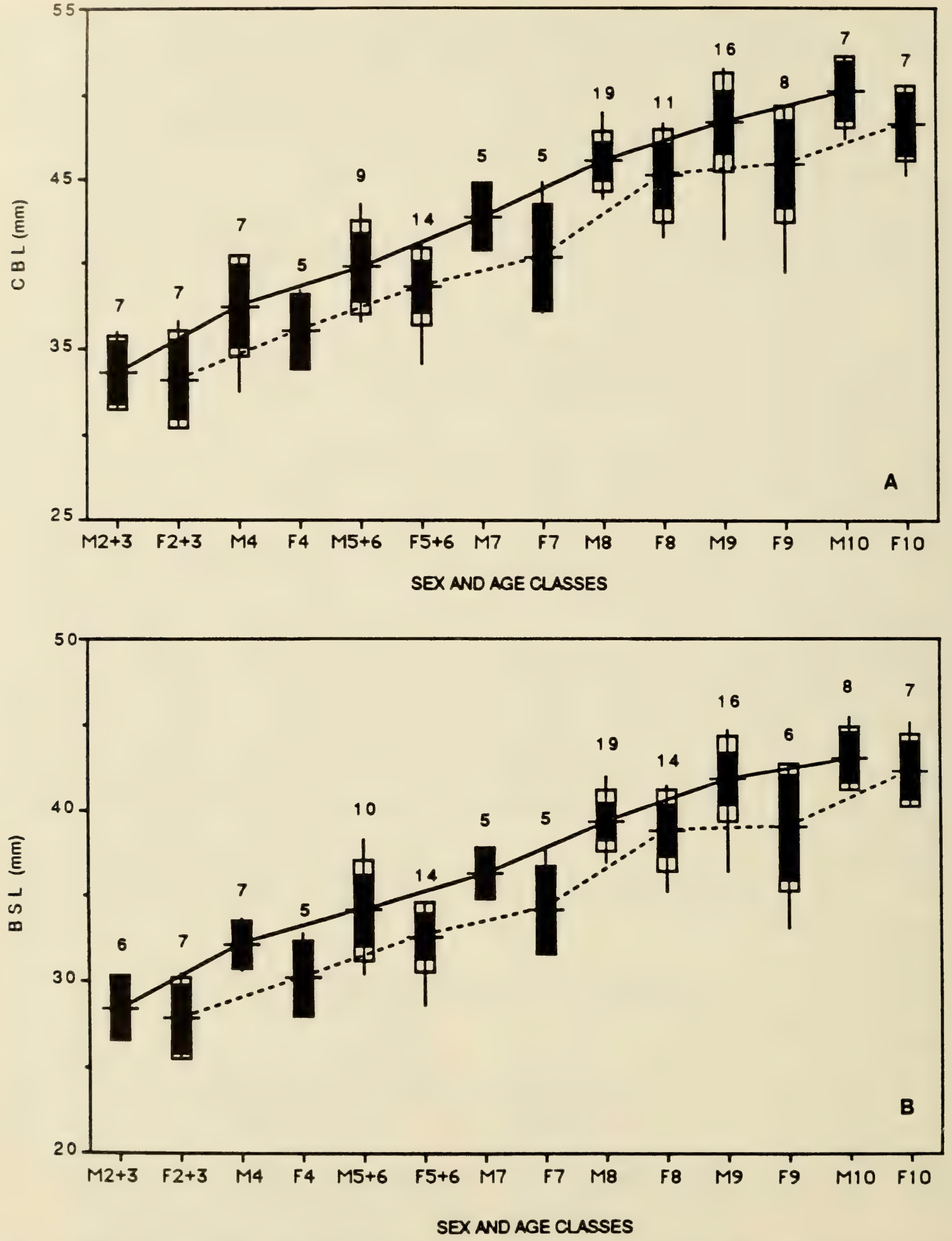

Fig. 1. Dice-Leraas diagrams for basilar length (BSL) and condylobasilar length (CBL) of both sexes and ten age classes of *Proechimys cuvieri* from Amapá, Brazil. The vertical lines are the range, horizontal lines the mean, black rectangles are two times the standard error of the mean, and white rectangles are the standard deviation. Solid lines connecting means portray the change among age classes of males; dotted lines are for females. See Table 2 for additional information.

8, 95% had reproduced at least once. We have no data that bear on actual time of maximal reproduction for our sample of female *P. cuvieri,* but if they follow the pattern for *P. brevicauda* the reproductive efforts of females could retard growth in comparison to males. Ultimately, however, by age class 10 females of *P. cuvieri,* in our sample, reach similar size of males (Fig. 1); they were smaller, but not significantly so, in most characteristics.

Variation among juveniles.—Not surprisingly, the contribution of age to variation among juveniles is large (50.51%) and suggests that relatively more growth is occurring from ages 2 to 7 than among adults of ages 8 to 10 (Table 1). Sex makes a small contribution (3.32%) to the total variation, as does the interaction term (2.23%). There is a large error term (44.1%) associated with variation among juveniles. The data indicate the unique feature that growth continues in these animals throughout life. The overall measures of skull length are always increasing (Fig. 1, Appendix 1). This happens throughout all adult age classes, even at the oldest individuals (age class 10), in which the teeth are extremely worn, many times down to their alveoli.

General trends.—That age contributes substantially to total variation, across all age classes, is not unexpected; the average age contribution is 68.6% (Table 1). Conversely, sex contributes little (1.46%), as does the interaction between sex and age (1.22%). After the contribution of age to variation, the error term accounts for the greatest amount (24.8%) of remaining variation. The percent contribution of age to total variance (all animals) is about 15% more for measures of skull length compared to those of width (Table 3). Sex appears to influence the two classes of measurements about equally. In juveniles (age 2–7), age has a greater effect (60%) upon length measurements than width and suggests that growth in length of the skull extends over several juvenile age classes. The percent contribution of sex to variation in length and width are similar and the variables that are significantly affected by sex include both length and width characteristics. However, for adults age has a slightly larger effect upon length variables, and sex contributes more to variation in length than to width characters.

Table 2.—Percent change in 10 variables from adult age classes for males (above) and females (below).

Variable	Age 8–9	Age 9–10
HBL	11.09	1.20
	4.19	2.90
CBL	5.02	3.72
	1.57	5.12
BSL	6.14	2.97
	0.33	8.54
PL	8.23	1.48
	2.64	5.50
D	7.00	3.99
	2.98	6.30
BLW	5.75	3.40
	−1.51	5.22
NL	6.38	2.34
	0.58	5.76
RB	6.05	2.17
	0.24	1.42
BB	2.71	3.37
	0.49	5.35
ML	6.02	2.97
	1.76	8.19

Straney (1978) reported that age has a slightly larger effect upon width characters than upon ones measuring cranial length among six species of carnivores and rodents (he did not include *Proechimys* in this comparison). We reexamined the data for just the rodents in his study, and discovered that age tends to influence length measurements more than measurements of width, as in our data. *P. cuvieri* may reach near-adult size in the measured breadth characters early in life, whereas growth in length continues within the age classes we examined. Thus, investigators might be able to use breadth measurements in a mixed-age sample to study

Table 3.—Average contribution of age and sex to cranial variables related to length and to width.

	All (2–10)		Juveniles (2–7)		Adults (8–10)	
	Age	Sex	Age	Sex	Age	Sex
Length	76.76	1.32	60.51	3.39	20.70	6.66
Width	66.53	1.41	39.89	3.92	19.86	2.90

geographic variation in *P. cuvieri*; length measurements might not be suitable for such analyses.

The magnitude of the error, or individual, component can be used for decisions for subsequent morphometric analyses (Straney 1978). The average percent contributions of age, sex, and interaction term to total variance for all age classes combined for *P. cuvieri* (Table 1) are similar to Straney's (1978) analysis of adult *P. longicaudatus*-group member, although he used only three characters. Straney considered error terms of 19–40% as small and thus such characters are useful for taxonomic comparisons because sex and age effects can be partitioned by making comparisons within one age or sex class. In cases where the error component is larger such partitioning is ineffective, and Straney recommends that, for studies of geographic variation, sexes and ages be pooled to increase sample sizes.

Within our sample of adult (ages 8–10) *P. cuvieri,* many characters have large error terms (19 of 25 are over 60%, Table 1). Overall, the error term is responsible for 73.4% (Table 1) of the total variation in adults in our study; the same percent error term was found for adults from a single population of *P. brevicauda* from northern Peru (Patton & Rogers 1983). In a population of *P. albispinus* from northeast Brazil the magnitude of the error term value was also similar (Pessôa & Reis 1991). Our study shows that age ($\bar{X}$ = 16.6%) and sex ($\bar{X}$ = 6.5%) terms contribute little, on average, to total variance among this now more homogeneous group. This indicates that individual variation within age and sex categories is high. The large amount of individual variation we detected may or may not affect the ability to separate *P. cuvieri* from other species of *Proechimys.* We did not make such comparisons. Patton & Rogers (1983) demonstrated that for two other species of *Proechimys,* with similar levels of sex and age variation as our sample, discrimination of two species improved by about 25% when age classes were analyzed separately.

We agree with Straney (1978) and Leamy (1983) that a variance component approach is useful, in determining how characters are treated in subsequent analyses, and in making decisions on whether to combine or separate age and sex classes. Ideally, one might wish to analyze geographic variation in *Proechimys* using separate age and sex classes. However, sample sizes may dictate, and variance component analysis support, the combination of adult classes for analyses of geographic variation.

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Appendix 1.—Descriptive statistics for 25 morphometric variables of *P. cuvieri,* with mean, standard deviation, coefficient of variation, and sample size (in parentheses) for males (above) and females (below) in each age class, all localities combined.

Variable	2–3	4	5–6	7	8	9	10
HBL	159.00–12.94	178.57–13.45	192.45–18.06	208.75–6.29	226.16–13.45	251.25–31.49	254.37–12.08
	8.14 (5)	7.53 (7)	9.39 (11)	3.01 (4)	5.95 (19)	12.53 (16)	4.75 (8)
	147.83–12.89	171.25–8.54	186.43–12.16	193.75–11.09	225.00–15.44	234.44–6.82	241.25–17.47
	8.72 (6)	4.99 (4)	6.52 (14)	5.72 (4)	6.86 (14)	2.91 (9)	7.24 (8)
TL	110.00–3.54	122.50–7.58	140.40–11.57	148.75–8.54	172.13–9.90	170.00–11.18	170.00–22.64
	3.21 (5)	6.19 (6)	8.24 (10)	5.74 (4)	5.75 (15)	6.58 (5)	13.32 (5)
	108.2–8.87	121.25–2.50	139.50–10.66	143.75–18.87	167.92–8.91	166.67–10.80	162.50–22.08
	8.20 (5)	2.06 (4)	7.64 (10)	13.13 (4)	5.31 (12)	6.48 (6)	13.59 (6)
HFL	36.4–1.95	40.71–0.95	43.90–3.25	45.00–2.58	47.82–1.55	48.73–2.09	48.38–2.20
	5.36 (5)	2.34 (7)	7.40 (10)	5.74 (4)	4.18 (17)	4.28 (15)	4.55 (8)
	35.6–3.36	40.50–1.73	41.57–1.95	43.75–2.99	45.86–1.92	46.22–1.86	44.50–2.62
	9.44 (5)	4.28 (4)	4.69 (14)	6.83 (4)	5.74 (14)	4.02 (9)	4.55 (8)
HFC	39.40–1.95	44.29–1.11	47.09–3.30	49.00–2.58	52.00–1.97	53.20–2.48	53.13–2.47
	4.95 (5)	2.51 (7)	7.01 (11)	5.27 (4)	3.79 (19)	4.67 (15)	4.66 (8)
	38.67–3.27	42.00–1.41	45.36–2.17	47.75–2.99	50.21–1.81	50.11–2.03	50.38–1.19
	8.45 (6)	3.37 (4)	4.78 (14)	6.25 (4)	3.59 (14)	4.05 (9)	2.36 (8)
EEH	18.20–1.10	18.71–1.38	19.50–2.59	19.00–0.82	20.68–2.06	20.27–0.59	20.12–0.64
	6.02 (5)	7.37 (7)	13.30 (10)	4.30 (4)	9.94 (19)	2.93 (15)	3.18 (8)
	17.67–1.63	18.25–1.26	19.07–0.83	20.00–0.00	19.50–1.16	19.78–0.97	20.25–1.58
	9.24 (6)	6.89 (4)	4.35 (14)	0.00 (4)	5.95 (14)	4.91 (9)	7.81 (8)
IEH	22.40–0.55	22.71–1.25	23.11–1.27	23.25–0.96	24.53–1.70	25.00–0.76	24.87–0.64
	2.45 (5)	5.52 (7)	5.49 (9)	4.12 (4)	6.93 (17)	3.02 (15)	2.58 (8)
	20.60–1.67	22.25–1.26	23.07–1.27	24.00–0.00	24.00–0.88	24.00–1.22	25.12–1.64
	8.12 (5)	5.66 (4)	5.50 (14)	0.00 (4)	3.65 (14)	5.10 (9)	6.54 (8)
W	113.40–21.51	143.14–13.45	206.10–54.48	234.50–28.92	307.25–41.20	387.81–86.48	397.71–56.21
	18.97 (5)	9.39 (7)	26.43 (10)	12.33 (4)	13.41 (17)	22.30 (15)	14.13 (8)
	92.00–29.72	131.50–14.84	164.21–38.50	196.00–30.94	318.21–54.72	362.78–76.36	351.29–57.15
	32.31 (5)	11.29 (4)	23.45 (14)	15.79 (4)	17.20 (14)	21.05 (9)	16.27 (8)
CBL	33.58–1.63	37.51–2.45	39.79–2.19	42.79–1.41	46.03–1.23	48.34–2.32	50.14–1.55
	4.87 (7)	6.53 (7)	5.51 (9)	3.29 (5)	2.68 (19)	4.79 (16)	3.08 (7)
	33.21–2.33	36.05–1.67	38.66–1.71	40.37–2.58	45.18–2.17	45.89–2.92	48.24–1.67
	7.03 (7)	4.63 (5)	4.43 (14)	6.40 (5)	4.81 (11)	6.37 (8)	3.47 (7)

Appendix 1.—Continued.

Variable	2–3	4	5–6	7	8	9	10
ZB	20.84–1.47	22.64–0.56	24.15–1.06	25.14–0.75	26.45–0.75	27.14–1.92	28.22–1.17
	7.05 (7)	2.46 (7)	4.41 (12)	2.98 (4)	2.82 (17)	7.08 (15)	4.76 (7)
	20.66–1.55	21.83–1.36	23.37–0.99	23.94–1.22	26.20–1.28	26.66–1.16	28.10–1.08
	7.49 (6)	6.21 (6)	4.22 (13)	5.10 (5)	4.90 (12)	4.37 (9)	3.84 (7)
BSL	28.43–1.37	32.18–0.84	34.14–2.40	36.38–0.97	39.38–1.22	41.80–1.96	43.04–1.31
	4.83 (6)	2.60 (7)	7.02 (10)	2.67 (5)	3.10 (19)	4.69 (16)	3.04 (8)
	27.82–1.85	30.19–1.66	32.60–1.51	34.17–2.01	38.85–1.84	38.98–3.14	42.31–1.57
	6.65 (7)	5.50 (5)	4.64 (14)	5.87 (5)	4.73 (14)	8.05 (6)	3.71 (7)
PL	13.45–0.98	15.53–0.75	16.52–0.97	17.93–0.55	19.32–0.98	20.91–0.94	21.22–1.00
	7.26 (7)	4.85 (8)	5.88 (12)	3.09 (5)	5.07 (19)	4.48 (15)	4.71 (8)
	13.48–1.52	15.68–2.15	16.14–1.23	16.95–1.00	18.95–0.95	19.45–1.36	20.54–0.72
	11.25 (6)	13.70 (6)	7.60 (14)	5.92 (5)	5.03 (14)	7.01 (8)	3.49 (8)
MTRL	4.34–0.26	5.09–1.01	6.69–0.23	6.12–1.02	8.64–0.27	8.76–0.46	8.68–0.41
	6.09 (7)	19.78 (7)	3.41 (12)	16.63 (4)	3.17 (18)	5.28 (16)	4.73 (8)
	4.36–0.23	4.36–0.16	6.60–0.27	6.53–0.30	8.55–0.23	8.47–0.39	8.68–0.41
	5.19 (7)	3.77 (7)	4.17 (13)	4.61 (5)	2.75 (13)	4.56 (7)	4.40 (6)
MB	7.01–0.68	7.63–0.30	8.05–0.62	8.35–0.66	9.16–0.67	10.03–0.62	10.65–0.61
	9.69 (6)	3.98 (7)	7.66 (12)	7.96 (4)	7.37 (19)	6.14 (16)	5.76 (8)
	6.93–0.65	6.89–0.60	7.73–0.57	7.50–0.41	9.22–0.77	9.61–1.07	10.39–0.30
	9.00 (6)	8.64 (7)	7.34 (13)	5.52 (5)	8.32 (12)	11.12 (7)	2.91 (8)
D	8.46–0.66	9.80–0.46	10.06–0.65	10.70–0.30	11.71–0.60	12.53–0.83	13.03–0.57
	7.85 (7)	4.72 (12)	6.49 (19)	2.78 (4)	5.11 (19)	6.63 (15)	4.36 (8)
	8.27–0.87	8.97–0.48	9.95–0.46	10.52–1.00	11.41–0.55	11.75–0.89	12.49–0.64
	10.49 (7)	5.34 (14)	4.67 (13)	9.47 (5)	4.85 (13)	7.57 (8)	5.13 (8)
IFL	4.06–0.51	4.49–0.37	4.97–0.40	4.91–0.47	5.59–0.43	5.94–0.77	5.97–0.51
	12.58 (7)	8.14 (8)	8.01 (12)	9.51 (5)	7.64 (20)	12.98 (16)	8.61 (8)
	3.86–0.55	4.29–0.43	4.63–0.40	4.93–0.42	5.32–0.43	5.43–0.39	5.86–0.74
	14.17 (7)	10.10 (7)	8.61 (14)	8.53 (5)	10.74 (14)	7.27 (9)	12.57 (8)
IFB	2.15–0.16	2.27–0.23	2.29–0.20	2.47–0.19	2.59–0.25	2.83–0.33	2.92–0.29
	7.60 (7)	10.13 (8)	8.72 (12)	7.79 (5)	9.62 (19)	11.78 (16)	10.07 (8)
	20.4–0.17	2.21–0.18	2.27–0.31	2.47–0.10	2.63–0.36	2.68–0.41	2.63–0.08
	8.23 (7)	8.32 (7)	13.79 (14)	4.20 (5)	13.75 (14)	15.14 (9)	3.20 (8)

Appendix 1.—Continued.

Variable	2–3	4	5–6	7	8	9	10
BLW	7.94–0.77	8.54–0.26	9.22–0.71	9.49–0.45	9.73–0.54	10.29–0.61	10.64–0.43
	9.71 (7)	3.00 (8)	7.70 (12)	4.79 (5)	5.52 (20)	5.92 (16)	4.09 (8)
	8.10–0.74	8.31–0.46	8.81–0.45	8.59–0.24	9.92–0.39	9.77–0.64	10.28–0.47
	9.16 (7)	5.58 (7)	5.15 (14)	2.77 (5)	5.00 (13)	6.56 (9)	4.54 (8)
IL	5.29–0.38	5.89–0.37	6.07–0.48	6.83–0.29	7.08–0.75	7.96–0.91	8.21–0.94
	7.10 (7)	6.32 (8)	7.88 (12)	4.32 (5)	10.66 (19)	11.37 (5)	11.50 (8)
	5.05–0.38	5.02–0.78	5.80–0.78	6.22–0.62	7.20–0.60	7.61–0.57	8.03–0.59
	8.56 (7)	15.48 (7)	16.46 (14)	10.02 (5)	8.38 (11)	7.45 (8)	7.34 (8)
IW	1.99–0.15	2.19–0.07	2.50–0.18	2.70–0.10	2.99–0.22	3.17–0.30	3.43–0.19
	7.65 (7)	3.40 (8)	7.10 (12)	3.70 (5)	7.35 (18)	9.30 (15)	5.68 (8)
	1.97–0.20	2.24–0.18	2.46–0.28	2.52–0.13	2.99–0.28	3.07–0.17	3.23–0.19
	10.13 (7)	8.24 (7)	11.44 (14)	5.17 (5)	9.25 (10)	5.47 (7)	8.02 (8)
NL	14.33–0.78	16.48–1.03	17.93–1.27	18.86–0.69	21.31–1.34	22.67–1.29	23.20–1.55
	5.45 (7)	6.24 (7)	7.07 (11)	3.66 (4)	6.29 (16)	5.71 (16)	6.69 (7)
	14.15–1.24	15.33–1.02	17.03–0.89	17.82–1.34	20.72–1.64	20.84–1.80	22.04–0.83
	8.74 (7)	6.68 (7)	5.22 (14)	7.50 (5)	7.93 (12)	8.65 (8)	3.76 (8)
RB	6.91–0.55	7.45–0.35	7.57–0.25	7.85–0.37	8.26–0.41	8.76–0.61	8.95–0.37
	8.01 (7)	4.72 (8)	3.29 (12)	4.66 (5)	5.02 (19)	6.95 (16)	4.09 (8)
	6.77–0.71	7.09–0.57	7.37–0.46	7.38–0.14	8.41–0.40	8.43–0.60	8.55–0.38
	10.55 (7)	8.04 (7)	6.22 (14)	1.95 (5)	4.81 (13)	7.16 (8)	4.39 (8)
IOC	10.20–0.75	11.07–0.43	11.35–0.50	12.16–0.70	12.38–0.52	12.91–0.91	13.60–0.25
	7.39 (7)	3.85 (8)	4.45 (12)	5.74 (5)	4.23 (20)	7.05 (16)	1.85 (8)
	9.96–0.44	10.54–0.81	11.21–0.50	11.40–1.04	12.41–0.59	12.74–0.47	12.79–1.19
	4.38 (7)	7.70 (7)	4.71 (14)	9.09 (5)	4.74 (14)	3.67 (9)	9.32 (8)
BB	17.05–0.75	18.15–0.66	18.98–0.68	19.66–0.46	20.66–0.70	21.22–0.88	22.02–0.60
	4.38 (7)	3.65 (8)	3.60 (12)	2.35 (5)	3.40 (20)	4.16 (16)	2.74 (8)
	16.90–0.67	17.74–0.71	18.61–0.47	18.58–0.79	20.46–0.88	20.56–0.84	21.66–0.51
	3.96 (7)	4.01 (7)	2.52 (14)	4.26 (5)	4.32 (14)	4.07 (9)	2.37 (8)

Appendix 1.—Continued.

Variable	2–3	4	5–6	7	8	9	10
ML	20.32–2.29	23.47–0.74	25.36–1.50	26.92–0.74	28.55–1.26	30.27–1.05	31.17–1.22
	11.29 (3)	3.16 (7)	5.90 (9)	2.73 (5)	4.41 (17)	3.46 (8)	3.92 (8)
	20.63–1.51	22.99–0.79	24.32–1.32	25.35–1.51	27.85–1.08	28.34–1.52	30.66–1.14
	7.31 (7)	3.45 (5)	5.42 (10)	5.95 (4)	3.88 (13)	5.37 (15)	3.73 (6)
LTRL	4.37–0.36	5.77–1.26	6.90–0.18	7.07–1.55	9.15–0.28	9.09–0.55	9.04–0.55
	8.15 (6)	21.87 (8)	2.64 (11)	21.90 (5)	3.04 (19)	6.03 (16)	6.04 (8)
	4.46–0.35	4.44–0.28	6.85–0.33	6.73–0.40	8.94–0.23	8.92–0.45	9.12–0.38
	7.92 (7)	6.21 (7)	4.78 (14)	5.91 (5)	2.62 (11)	5.01 (9)	4.16 (7)

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

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Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 25 June 1992 in Vol. 49, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these Applications is invited for publication in the *Bulletin,* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2788	*Mopsea* Lamouroux, 1816 (Cnidaria, Anthozoa): proposed designation of *Isis encrinula* Lamarck, 1815 as the type species.
2801	*Potamolithus* Pilsbry, 1896 (Mollusca, Gastropoda): proposed confirmation of *P. rushii* Pilsbry, 1896 as the type species.
2526	*Strombiformis albus* Da Costa, 1778 (currently *Melanella* (*Balcis*) *alba*; Mollusca, Gastropoda): proposed conservation of the specific name.
2789	*Amicytheridea* Bate, 1975 (Crustacea, Ostracoda): proposed designation of *Amicytheridea triangulata* Bate, 1975 as the type species.
2794	*Gerris paludum* Fabricius, 1794 (currently *Aquarius paludum*; Insecta, Heteroptera): proposed conservation of the specific name.
2772	*Chrysobothris* Eschscholtz, 1829 and *Dicerca* Eschscholtz, 1829 (Insecta, Coleoptera): proposed conservation as the correct original spellings.
2786	TACHINIDAE Fleming, 1821 (Insecta, Coleoptera) and TACHINIDAE Robineau-Desvoidy, 1830 (Insecta, Diptera): proposed removal of homonymy, and TACHYPORIDAE MacLeay, 1825 (Insecta, Coleoptera): proposed precedence over TACHINUSIDAE Fleming, 1821.
2803	*Copromyza limosa* Fallén, 1820 (currently *Leptocera* (*Rachispoda*) *limosa*; Insecta, Diptera): proposed replacement of lectotype, so conserving usage of the specific name and also that of *Leptocera* (*Rachispoda*) *lutosa* (Stenhammar, 1855).
2804	*Drosophila putrida* Sturtevant, 1916 (Insecta, Diptera): proposed replacement of the holotype by a neotype.
2706	EPHYDRIDAE Zetterstedt, 1837 (Insecta, Diptera): proposed precedence over GYMNOMYZIDAE Latreille, 1829.
2718	*Clidastes* Cope, 1868 (Reptilia, Sauria): proposed designation of *Clidastes propython* Cope, 1869 as the type species.
2784	*Procellaria gigantea* Gmelin, [1789] (currently *Macronectes giganteus*; Aves, Procellariiformes): proposed conservation of usage of the specific name by designation of a neotype.

The following Opinions were published on 25 June 1992 in Vol. 49, Part 2 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1675 *Amphiporus* Ehrenberg, 1831 (Nemertea): *Planaria lactiflorea* Johnston, 1828 designated as the type species.

1676 *Lepidomenia* Kowalevsky *in* Brock, 1883 (Mollusca. Solenogastres): *Lepidomenia hystrix* Marion & Kowalevsky *in* Fischer, 1885 designated as the type species.

1677 *Haustator* Montfort, 1810 (Mollusca, Gastropoda): conserved.

1678 *Helicarion* Férussac, 1821 (Mollusca, Gastropoda): conserved, and *Helicarion cuvieri* Férussac, 1821 designated as the type species.

1679 *Kobeltia* Seibert, 1873 (Mollusca, Gastropoda): *Arion hortensis* Férussac, 1819 confirmed as the type species.

1680 *Buthus vittatus* Say, 1821 (currently *Centruroides vittatus*), *Centrurus hentzi* Banks, 1904 (currently *Centruroides hentzi*) and *Buthus vittatus* Guérin Méneville, [1838] (currently *Bothriurus vittatus*) (Arachnida, Scorpionida): specific names conserved.

1681 *Vatellus* [Aubé], 1837 (Insecta, Coleoptera): conserved.

1682 *Plusia falcifera* Kirby, 1837 (currently *Anagrapha falcifera*; Insecta, Lepidoptera); specific name conserved.

1683 *Simulium* (*Nevermannia*) *juxtacrenobium* (Insecta, Diptera): specific name first available from the intended original description by Bass & Brockhouse, 1990.

1684 *Lepomis* Rafinesque, 1819 (Osteichthyes, Perciformes): gender fixed as masculine.

1685 *Rana sphenocephala* Cope, 1886 (Amphibia, Anura): given precedence over *Rana utricularius* Harlan, 1826.

1686 *Natrix gemonensis* Laurenti, 1768 (currently *Coluber gemonensis*), *Coluber viridiflavus* Lacépède, 1789 and *Coluber helveticus* Lacépède, 1789 (currently *Natrix natrix helvetica*) (Reptilia, Serpentes): specific names conserved.

1687 *Phorusrhacos* Ameghino, 1887 (Aves, Gruiformes): not suppressed.

1688 *Coccyzus euleri* Cabanis, 1873 (Aves, Cuculiformes): specific name conserved.

NOTICE

The Association of Systematics Collections will hold its 1993 Annual Meeting on 7–9 May, 1993, in Pittsburgh, Pennsylvania at the Carnegie Museum of Natural History. The theme is "Public Relations for Systematic Collections and Research." The featured event will be a workshop on building local community support for collections and collections-based research, including suggestions for working with trustees and friends' groups. There will also be an in-depth discussion of the draft documents of "Systematics Agenda 2000" (the effort to determine research needs and priorities in systematics), with a session on implementation strategies. A business meeting and discussion of NSF programs will be held on 7 May. A riverboat cruise will be the stage for the annual banquet and award ceremony on 8 May. There will be opportunities to visit the Carnegie collections and the Hunt Institute for Botanical Documentation. For program and hotel information, contact:

ASC
730 11th Street N.W., 2nd Fl.,
Washington, D.C. 20001 U.S.A.
Phone: (202) 347-2850
Fax: (202) 347-0072

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

Two new species of *Chrysolaena* from Brazil (Vernonieae: Asteraceae) Harold Robinson 657

Three new species of *Justicia* (Acanthaceae) from Brazil Dieter C. Wasshausen 664

Observations on and redescription of *Meiomenia arenicola* Salvini-Plawen, 1985 (Mollusca: Aplacophora), an interstitial solenogaster from Fort Pierce, Florida M. Patricia Morse and Jon L. Norenburg 674

A tale of two species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae) Michael Vecchione, Bruce H. Robison, and Clyde F. E. Roper 683

New species and records of Phyllodocidae (Polychaeta) from the continental shelf and slope off California James A. Blake 693

New polychaetous annelids of the families Nereididae, Hesionidae, and Nephtyidae from the Santa Maria Basin, California, with a redescription of *Glycera nana* Johnson, 1901 Brigitte Hilbig 709

Polychaeta from deep-sea hydrothermal vents in the eastern Pacific. III. A new genus and two new species of Spionidae from the Guaymas Basin and Juan de Fuca Ridge with comments on a related species from the western North Atlantic James A. Blake and Nancy J. Maciolek 723

Deltamysis holmquistae, a new genus and species of Mysidacea from the Sacramento-San Joaquin estuary of California (Mysidae: Mysinae: Heteromysini) Thomas E. Bowman and James J. Orsi 733

Diastylopsis goekei, a new species (Crustaceae: Cumacea: Diastylidae) from Antarctic waters Daniel Roccatagliata and Richard W. Heard 743

Remarks on distribution and hosts for symbiotic crustaceans of the Mexican Pacific (Decapoda and Isopoda) Ernesto Campos, Alma Rosa de Campos, and Jorge Ramirez 753

Reexamination of the material of *Munida* Leach (Crustacea: Anomura: Galatheidae) collected by the H.M.S. *Challenger* (1872–1876) along the Brazilian coast Gustavo Augusto S. de Melo-Filho and Gustavo Augusto S. de Melo 760

Pinnaxodes gigas, a new species of pinnotherid crab from the Gulf of California (Decapoda: Brachyura: Pinnotheridae) Timothy M. Green 775

A new crawfish of the genus *Orconectes* from east-central Mississippi and adjacent Alabama (Crustacea: Decapoda: Cambaridae) J. F. Fitzpatrick, Jr. 780

The freshwater crabs and palaemonid prawns (Crustacea: Decapoda) of Batam Island, Riau Archipelago, Indonesia, including descriptions of two new species Peter K. L. Ng 788

A reassessment of *Pagurus tricarinatus* (Stimpson, 1858) (Crustacea: Decapoda: Anomura: Paguridae) Patsy A. McLaughlin 795

A review of the genus *Chloronia* in Costa Rica, with the description of two new species (Neuropterida: Megaloptera: Corydalidae) Oliver S. Flint, Jr. 801

Caprovesposus from the Oligocene of Russia: the pelagic acronurus presettlement stage of a surgeonfish (Teleostei: Acanthuridae) Alexandre F. Bannikov and James C. Tyler 810

A new lizard of the genus *Arthrosaura* (Teiidae) from southern Venezuela Maureen A. Donnelly, Roy W. McDiarmid, and Charles W. Myers 821

Diagnosis of a hybrid antbird (*Phlegopsis nigromaculata* × *Phlegopsis erythroptera*) and the rarity of hybridization among suboscines Gary R. Graves 834

Systematics and biogeography of the New England cottontail, *Sylvilagus transitionalis* (Bangs, 1895), with the description of a new species from the Appalachian Mountains Joseph A. Chapman, Kenneth L. Cramer, Nico J. Dippenaar, and Terence J. Robinson 841

Distribution, geographic variation, and systematic relationships within *Nelsonia* (Rodentia: Sigmodontinae) Mark D. Engstrom, Oscar Sánchez-Herrera, and Guillermina Urbano-Vidales 867

Sex and age components of variation in *Proechimys cuvieri* (Rodentia: Echimyidae) from northern Brazil Marcia Lara, Michael A. Bogan, and Rui Cerqueira 882

International Commission on Zoological Nomenclature 894

Notice 896

Table of Contents, Volume 105 iv

Index to New Taxa, Volume 105 viii

23 286 SI XL 436
08/93 98115

SMITHSONIAN INSTITUTION LIBRARIES

LIBRARIES SMITHSONIAN INSTITUTION
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